

# PHYLOGENETIC SYSTEMATICS OF THE NOTASPIDEA (OPISTHOBANCHIA) WITH REAPPRAISAL OF FAMILIES AND GENERA

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## ABSTRACT

Character states for 57 qualitative characters are described for the opisthobranch order Notaspidea and their distribution among Recent genera tabulated. Characters employed pertain to behavior, body form, mantle, shell, jaws, radula, comparative anatomy of the gut and reproductive system. Primitive and advanced conditions for each character are inferred on the basis of outgroup comparisons. Data from this matrix are used to construct a phylogenetic hypothesis by application of the Hennigian method and rule of parsimony. This phylogenetic cladogram is compared to an unweighted, computer-generated dendrogram. Data from these cladistic and phenetic analyses are employed in reappraising higher taxa of the order. Two suborders, three families, two subfamilies, two tribes and 11 genera are recognized. Characters defining each taxon are briefly enumerated and examined to consider inter-relations; this consideration extends to reconsideration of synonymous genera.

Opisthobranch gastropods belonging to the order Notaspidea display considerable heterogeneity of body form yet all possess a bipinnate gill on the right side which lies longitudinally between the mantle and foot and is attached to the body for the greater part of its length. The significance of this (symplesiomorphic) side-gilled condition is that it is a necessary intermediate stage in the transition from the primitive, shelled "tectibranch" grade of opisthobranch body organization to the advanced "nudibranch" one as seen in Recent opisthobranchs belonging to the order Anthobranchia (= Doridacea). Indeed such a transitional series is seen in the gill/anal interrelations of modern deep-sea anthobranch nudibranchs belonging to the primitive genus *Bathydoris* (Evans, 1914; Minichev, 1970). Notaspideans are thus prime candidates as ancestors of anthobranch nudibranchs (Odhner, 1939; Ghiselin, 1966; Minichev, 1970; Faulkner and Ghiselin, 1983).

The Notaspidea is a comparatively small order. To the end of 1985, the actual number of described species (including taxa proposed with subordinate status) was 236. No malacologist knows how many biological species exist and regional monographs are sorely needed. The higher classification of the order had turbulent beginnings (summarized by Willan, 1983), but it has now stabilized largely

due to Odhner's (1939) and Burn's (1962) thorough taxonomic revisions (see Table 1). The classification of the order

**Table 1.** Hitherto proposed higher classification of the Notaspidea.

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Order Notaspidea Fischer, 1883
Suborder Umbraculacea Dall, 1889
Family Tylodinidae Gray, 1847
Genus <i>Tyloдина</i> Rafinesque, 1819
Genus <i>Tyloдина</i> Mazzarelli, 1898
Family Umbraculidae Dall, 1889
Genus <i>Umbraculum</i> Schumacher, 1817
Suborder Pleurobranchacea Menke, 1828
Family Pleurobranchidae Menke, 1828
Subfamily Berthellinae Burn, 1962
Genus <i>Berthella</i> Blainville, 1825
Genus <i>Bathyberthella</i> Willan, 1983
Genus <i>Pleurehdera</i> Ev. Marcus and Er. Marcus, 1970
Genus <i>Berthellina</i> Gardiner, 1936
Subfamily Pleurobranchinae Férussac, 1822
Genus <i>Pleurobranchus</i> Cuvier, 1805
Family Pleurobranchaeidae Pilsbry, 1896
Genus <i>Pleurobranchella</i> Thiele, 1925
Genus <i>Pleurobranchaea</i> Meckel in Leue, 1813
Genus <i>Euselenops</i> Pilsbry, 1896

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presented in Table 1 is founded on the latest scheme (Burn, 1962) and it incorporates genera described subsequently (Er. Marcus and Ev. Marcus, 1970; Willan, 1983) plus alterations and emendments resulting from papers by Thompson (1970), Baba and Hamatani (1971) and Willan (1977, 1978, 1983). Two suborders, four families and 11 genera are currently recognized (Figs. 1-8).

Much of the literature on notaspidean taxonomy stems from collections made by early exploring expeditions and subsequent literature is widely scattered. The primary literature sources (i.e. those chiefly consulted for distribution of character states) are given in Table 2.

Phylogenetic classifications, as based on Hennigian principles, serve as the best reference systems for the diverse knowledge we now have and are gaining about the evolution of organisms (Hennig, 1966). Their strength lies in their insistence that the taxonomic classification adopted constantly reflect estimates of speciation events in nature (Wiley, 1981). In the past, definitions of higher taxa in the Notaspidea were based on too few (sometimes only one) characters, some of which were homeoplasies, and critical outgroup comparisons were not made so the taxa are unfortunately not amenable to rigorous phylogenetic treatment. As Ev. Marcus and Gosliner (1984) have remarked, incomplete descriptions, which have plagued notaspidean taxonomy, are no

longer acceptable. This paper amasses data on 57 qualitative characters and reports the distribution of their states among the eleven notaspidean genera. Primitive and advanced conditions for each character are inferred on the basis of outgroup comparisons. Fortunately this is possible both within the Notaspidea and beyond that to other opisthobranch orders because parallel evolutionary developments have occurred independently many times (Willan and Morton, 1984, p. 9; Gosliner and Ghiselin, 1984). A cladogram is presented, and it is compared with a computer-generated dendrogram of these same data in simple, phenetic form. This paper attempts then, to provide a phylogenetic classification for the Notaspidea (i.e. one that reflects the best estimate of the evolutionary history of the order) (Brundin, 1968).

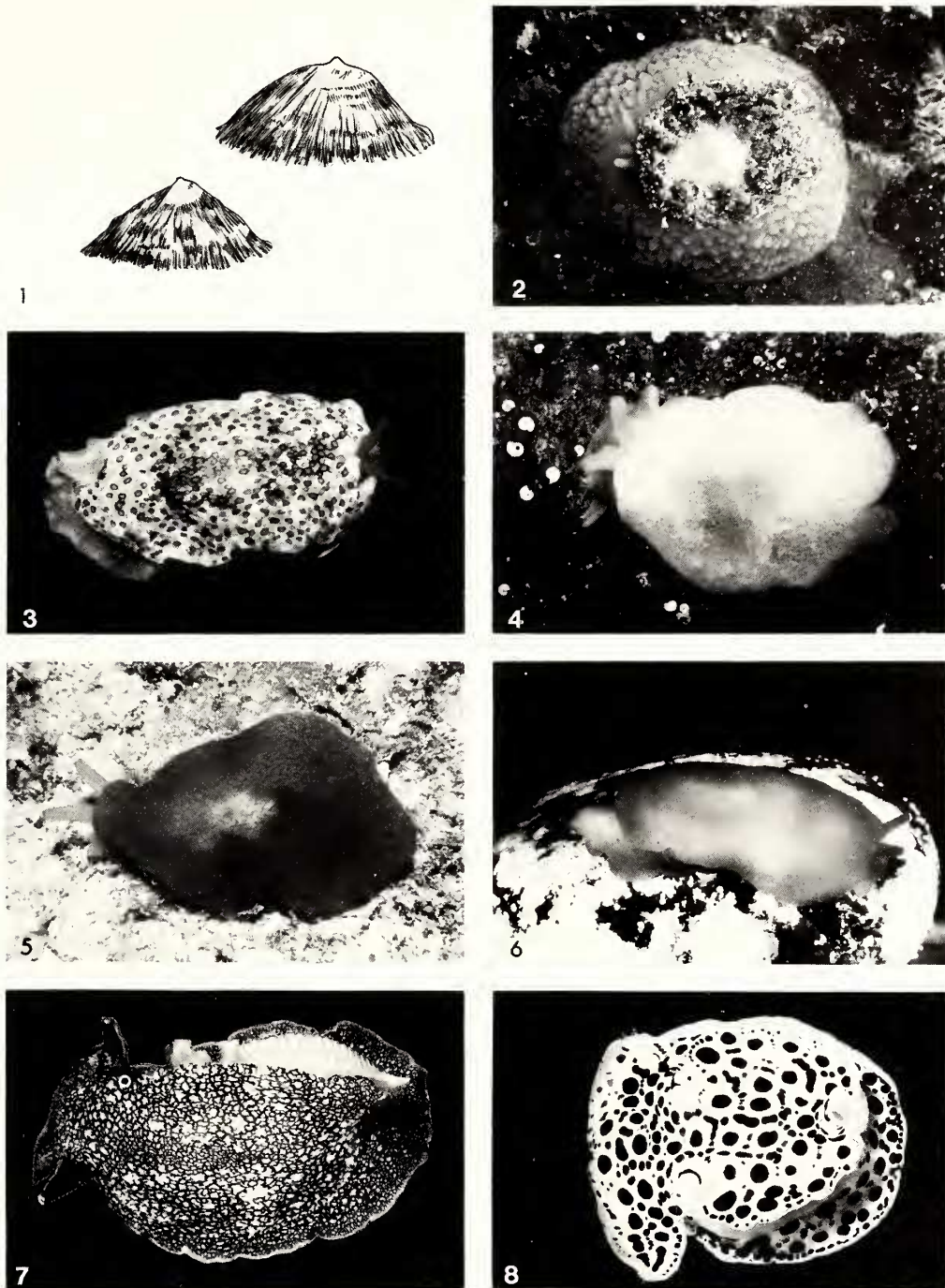
## METHODS

A set of data for the distribution of 57 qualitative characters was compiled for each of the 11 notaspidean genera listed in Table 1. Characters selected pertain to behavior, body form, mantle, shell, jaws, radula, alimentary and reproductive systems (see Table 3). Characters selected were those that have in the past been considered as taxonomically significant within the order or those which the author believes will be significant in future phylogenetic analyses (e.g. those relating to mantle morphology and behavior that can only be observed or studied in life). Unfortunately characters to do with food or feeding (see review by Willan, 1984a), mantle histology (see review by Thompson and Colman, 1984), sperm ultrastructure (Thompson, 1973; Healy and Willan, 1984), nervous or circulatory systems, or larval studies could not be incorporated because of lack of comparative information. Data on the distribution of character states were collated from personal examinations of the following notaspidean species: *Tylodina corticalis* (Tate); *Umbraculum umbraculum* (Lightfoot); *Berthella pellucida* (Pease); *B. ornata* (Cheeseman); *B. medietas* Burn; *B. americana* (Verrill); *B. martensi* (Pilsbry); *Bathyberthella zelandiae* Willan; *B. antarctica* Willan and Bertsch; *Pleurehdera haraldi* (Er. Marcus and Ev. Marcus); *Berthellina citrina* (Rüppell and Leuckart); *Pleurobranchus grandis* Pease; *P. albigitatus* (Bergh); *P. forsskali* Rüppell and Leuckart; *P. mamillatus* Quoy and Gaimard; *P. peronii* Cuvier; *Pleurobranchella alba* (Guangyu and Si); *P. nicobarica* Thiele; *Pleurobranchaea maculata* (Quoy and Gaimard); *Euselelops luniceps* (Cuvier). Extensive recourse to the literature was made as well (see Table 2).

Following the method of Hennig (1966), a phylogenetic cladogram was manually constructed for the order. Only unique, derived or "advanced" (apomorphic) characters, as determined in the section on character states, were employed in this analysis and branching systems followed the law of parsimony. This phylogenetic cladogram was then compared with a computer-generated phenetic dendrogram. In amassing the character state distributions to produce this dendrogram (Tables 4, 5), no "weighting" of characters as regards their level of relative primitiveness or advancement

**Table 2.** Primary literature sources consulted for distribution of character states amongst notaspidean genera.

Genus	Literature Sources
<i>Tylodina</i>	Vayssière, 1883; Mazzarelli, 1898 (as <i>Tylodinel-la</i> ); Burn, 1960; MacFarland, 1966; Gosliner, 1981; Ev. Marcus, 1985
<i>Anidolyta</i> nov.	Odhner, 1939 (as <i>Tylodinel-la</i> ); Bertsch, 1980 (as <i>Roya</i> ); Ev. Marcus, 1985
<i>Umbraculum</i>	Moquin-Tandon, 1870; Vayssière, 1885; O'Donoghue, 1929; Pruvot-Fol, 1954; Thompson, 1970; Ev. Marcus, 1985
<i>Berthella</i>	Vayssière, 1898 (as <i>Bouvieria</i> ); Odhner, 1939; Burn, 1962; Willan, 1984b; Ev. Marcus, 1984
<i>Bathyberthella</i>	Willan, 1983; Willan and Bertsch, 1987
<i>Pleurehdera</i>	Er. Marcus and Ev. Marcus, 1970; Willan, 1984b
<i>Berthellina</i>	Lacaze-Duthiers, 1859 (as "Pleurobranche orange"); Vayssière, 1898 (as <i>Berthella</i> ); Bergh, 1905 (as <i>Berthella</i> ); Gardiner, 1936; Burn, 1962; Ev. Marcus and Er. Marcus, 1967; Thompson, 1970; Willan, 1983
<i>Pleurobranchus</i>	Bergh, 1897, 1898, 1902, 1905; Vayssière, 1898; Thompson and Slinn, 1959; MacFarland, 1966; Thompson, 1970; Ev. Marcus, 1984
<i>Pleurobranchella</i>	Thiele, 1925; O'Donoghue, 1929 (as <i>Pleurobranchoides</i> ); Eales, 1938; Willan, 1977; Ev. Marcus and Gosliner, 1984
<i>Pleurobranchaea</i>	Bergh, 1897; Vayssière, 1901; MacFarland, 1966; Willan, 1983; Ev. Marcus and Gosliner, 1984
<i>Euselelops</i>	Bergh, 1897, 1905 (as <i>Oscaniopsis</i> ); Vayssière, 1901 (as <i>Oscaniopsis</i> ); O'Donoghue, 1929; Ev. Marcus and Gosliner, 1984



**Figs. 1-8.** Type species of notaspidean genera. **Fig. 1.** *Tyrodina perversa* (Gmelin): profile of two shells, both 14 mm in maximum length, from Guéthary, near Biarritz, Bay of Biscay, France; redrawn from Pruvot-Fol and Fischer-Piette, 1934: 146. **Fig. 2.** *Umbraculum umbraculum* (Lightfoot): juvenile, extended crawling length of animal 48 mm; found at low tide, Boat Harbour, Cronulla, Sydney, central New South Wales, Australia, 20 May 1979; photograph by R. C. Willan. **Fig. 3.** *Pleurobranchus peronii* Cuvier: length 65 mm; found at low tide, Amity, Moreton Bay, southern Queensland, Australia, 10 November 1981; photograph by R. C. Willan. **Fig. 4.** *Berthella plumula* (Montagu): length 21 mm, found at Knysna, South Africa, May 1984; photograph by T. M. Gosliner. **Fig. 5.** *Pleurehdera haraldi* Er. Marcus and Ev. Marcus: length 40 mm, 3 m, Enewetak Island, Enewetak Atoll, Marshall Islands, 19 September 1981; photograph by S. Johnson. **Fig. 6.** *Berthellina engeli* Gardiner: length 25 mm, found at low tide, Santa Cruz Island, southern California, 23 August 1985; photograph by P. A. Dunn. **Fig. 7.** *Pleurobranchaea meckelii* (Blainville): length 100 mm, 50 m, Gulf of Genoa, Ligurian Sea, northwestern Italy, August 1978; photograph by R. Cattaneo-Viatti. **Fig. 8.** *Euselenops luniceps* (Cuvier): length 60 mm, found at low tide, North Stradbroke Island, southern Queensland, Australia, 29 September 1981; photograph by R. C. Willan.

**Table 3.** Relative Plesiomorphy and Apomorphy of Characters used for Cladistic Analysis of Notaspidea.

Plesiomorphic	Apomorphic
1. Shell present	Shell absent
2. Shell located externally	Shell internal beneath mantle
3. Shell calcified	Shell without calcification
4. Periostracum smooth, adhering to shell	Periostracum rough, lamellate
5. Muscle scar incomplete	Muscle scar forming a complete ring
6. Shell circular in shape	Shell rectangular
7. Shell (of Umbraculacea) conical	Shell (of Umbraculacea) flattened or plate-like
8. Shell (of Pleurobranchacea) auriculate-oval	Shell (of Pleurobranchacea) spatulate-triangular
9. Shell located centrally relative to body	Shell located anteriorly (rarely posteriorly) relative to body
10. Shell large relative to body	Shell small relative to body
11. Mantle and shell same size	Mantle larger than shell
12. Mantle smooth in texture	Mantle pustulose or puckered
13. Spicules lacking from mantle	Spicules embedded in mantle
14. Anterior border of mantle entire	Anterior border of mantle emarginate or cleft
15. Posterior border of mantle entire	Posterior border of mantle cleft ( <i>Euselelops</i> only)
16. Mantle margin entire	Mantle margin crenulate ( <i>Tylo dinella</i> ) deeply serrate ( <i>Umbraculum</i> )
17. Mantle incapable of autotomy	Mantle capable of autotomy (Some <i>Berthella</i> spp. only)
18. Separation of mantle anteriorly from oral veil	Fusion of mantle anteriorly with oral veil
19. Separation of mantle posteriorly from foot	Fusion of mantle posteriorly with foot
20. One pair of oral tentacles	Two pairs of oral tentacles ( <i>Umbraculum</i> only)
21. Oral tentacles separate	Oral tentacles joined by oral veil
22. Oral veil relatively narrow with respect to body	Oral veil relatively broad with respect to body
23. Oral veil without papillae	Papillae along anterior edge of oral veil
24. Rhinophores separated ( <i>Umbraculum</i> only)	Rhinophores together but without any basal fusion ( <i>Tylo dinidae</i> ) Rhinophores together with bases fused ( <i>Pleurobranchacea</i> ) Rhinophoral tips regularly pulsate in living specimen ( <i>Pleurobranchus</i> only)
25. Rhinophores without rhythmic activity in living specimen	
26. Upper surface of foot smooth	Upper surface of foot with large pustules ( <i>Umbraculum</i> only)
27. No pedal gland	Pedal gland present on sole of foot of sexually mature specimens
28. Pedal gland small relative to foot length	Pedal gland large relative to foot length ( <i>Pleurehdera</i> only)
29. No caudal spur	Caudal spur present posteriorly on upper side of foot (some <i>Pleurobranchaea</i> spp. only)
30. Foot without a vertical cleft anteriorly	Foot with a deep, vertical cleft anteriorly ( <i>Umbraculum</i> only)
31. Gill located in right posterior quadrant of body	Gill extending from left antero-lateral corner of body almost to posterior midline ( <i>Umbraculum</i> only)
32. Gill attached to body for half its length	Gill attached to body for almost entire length ( <i>Umbraculum</i> only)
33. Gill with smooth rachis	Gill rachis with row of pustules
34. Anus at posterior end of gill basement membrane	Anus well behind posterior end of gill basement membrane ( <i>Umbraculum</i> only) Anus in front of end of gill basement membrane Anus opening at end of anal tube ( <i>Umbraculum</i> only)
35. Anus opening flush with body	
36. Mouth not in pedal cleft	Mouth in vertical pedal cleft ( <i>Umbraculum</i> only)
37. Buccal mass capable of protrusion during feeding	Buccal mass non-protrusible ( <i>Umbraculum</i> only)
38. No median buccal (= dorsal accessory) gland	Median buccal gland present
39. Radula with rachidian row	Radula without rachidian row
40. No denticle at base of lateral radular teeth	Single denticle at base (of at least some) lateral radular teeth
41. No accessory denticle on blade of lateral radular teeth	Single accessory denticle on blade of lateral radular teeth ( <i>Pleurobranchaea</i> only)
42. Lateral radular teeth not lamellate	Two or more denticles on blade of lateral radular teeth (i.e. laterals lamellate)
43. Labial cuticle with two separate thickenings (jaws)	Labial cuticle with a continuous, thickened ring
44. Mandibular elements oval or polygonal	Mandibular elements elongate with a pair of lateral projections (i.e. elements cruciform)
45. Blades of mandibular elements denticulate	Blades of mandibular elements smooth
46. Monaulic reproductive condition ( <i>Tylo dina</i> only)	Diaulic or triaulic reproductive condition

Table 3. (continued)

Plesiomorphic	Apomorphic
47. No flaps surrounding genital apertures	Enlarged flaps surrounding genital apertures in sexually mature specimens ( <i>Pleurobranchus</i> only)
48. External ciliated, autospermal groove present on penis	No autospermal groove
49. Penis at base of right anterior tentacle	Penis in vertical cleft in anterior midline, immediately below rhinophores and above mouth ( <i>Umbraculum</i> only)
Penis on right side in front of anterior end of gill	Penis able to be protruded for copulation
50. Penis non-protrusible	Penis with papillae on outer surface
51. Penis smooth	One allosperm receptacle only (bursa copulatrix)
52. Two allosperm receptacles present (bursa copulatrix and receptaculum seminis)	
53. When two allosperm receptacles are present, the receptaculum seminis arises low down off the vagina near female genital aperture	When two allosperm receptacles are present, the receptaculum seminis arises high up off the vagina near base of bursa copulatrix
54. Prostate gland surrounds or ensheaths autosperm canal or duct	Prostate gland present as a distinct organ
55. No penial gland	Penial gland present
56. Penial sac absent	Muscular penial sac present
57. Vas deferens does not coil within penial sac	Extensive coiling of vas deferens within penial sac

was made. Forty-five of the characters were initially coded as binary attributes (numbers 1, 2, 3, 4, 6, 7, 8, 11, 13, 14, 15, 17, 18, 19, 20, 21, 23, 25, 26, 27, 28, 29, 30, 33, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 47, 48, 50, 51, 52, 53, 55, 56 and 57), nine were coded as disordered multistate attributes (numbers 9, 10, 12, 16, 31, 32, 34, 49 and 54) and four were coded as ordered multistate attributes (numbers 5, 22, 24 and 46). A phenetic analysis using the information statistic "TAXON" program (Ross *et al.*, 1983) was then performed. Thirteen of the characters (numbers 3, 8, 11, 14, 17, 29, 33, 39, 40, 45, 51, 52, 55), originally classified as binary attributes, had to be reclassified as disordered multistate attributes for this computer program because both the two binary states existed together in some genera (e.g. a caudal spur is present in some species of *Pleurobranchaea* but not others) and the program could handle only the 0 or 1 states, not the (0,1) combination.

## CHARACTER STATES AND ANALYSES

### SHELL

The presence of an external shell in umbraculacean genera was the reason for the early splitting of the Notaspidea into "tectibranch" and "nudibranch" members (Cuvier, 1812, 1817). This artificial partitioning (based on evolutionary grades instead of clades), which denied the existence of an internal shell in pleurobranchs, was soon abandoned as more basic anatomical resemblances came to light. Whilst the shell *per se* of the Notaspidea is unmistakably a plesiomorphy, its actual shape has been much modified from the multispiral form that must have been possessed by the ancestral gastropod that gave rise to this order.

Notaspideans' shells, unlike those of other opisthobranch orders, never display heterostrophy. However, the extreme evolutionary divergence between the two suborders is manifestly evident in their shells. Shells of the Umbraculacea are external and limpet-like (the teleoconch has

essentially a circular aperture). The protoconch of both *Tylodina* (Figs. 9-11) and *Umbraculum* (Figs. 12-14) is anisotropically coiled with the spire (approximately 1.5 whorls) visible to the left of the teleoconch's (and animal's) midline. This sinistrality of the protoconch is evidence of hyperstrophy of larval shells. The only differences between these genera are that in *Tylodina*, the protoconch is narrower with a more elevated axis and the teleoconch is conical whereas in *Umbraculum*, the protoconch is broader and more depressed, its axis is relatively lower and the teleoconch is excessively flattened. The patelliform shell of umbraculaceans (particularly that of *Tylodina* and *Anidolyta*) is remarkably convergent with that of some pulmonates (e.g. siphonarids belonging to the genus *Williamia* (Marshall, 1981; Rehder, 1984). By contrast, shells of the Pleurobranchacea are (in members of the subfamily Pleurobranchinae where they are retained) internal and auriculate (the shell is essentially an exaggerated body whorl) in shape, and coiling is dextral. The larval shell (Figs. 15, 16), which consists of less than one whorl, is slung to the right of the teleoconch's (and animal's) midline. Because both the protoconch and teleoconch coil to the right, the whole shell is orthostrophic. Of course, neither umbraculaceans nor pleurobranchs possess an operculum, so interpretation of the animal's bodily organization must come from studies on larval animal-shell relationships during ontogeny. Then it can be ascertained whether shell shape is due to either anisostrophic coiling or detorsion, or both. Throughout the order, protoconchs are always spirally coiled, that is "type B" of Thorson (1946) and Soliman (1977) or "shell-type 1" of Thompson (1961) (Burn, 1960; Thompson, 1961; Hartley, 1964). The protoconch of umbraculaceans is sinistral revealing, I suggest, an underlying (plesiomorphic) hyperstrophy. That of Pleurobranchaceans is dextral by contrast. This dextrality is certainly an apomorphy and it probably represents a secondary detorsional symmetry imposed on the basic opisthobranch hyperstrophy. This switch in protoconch structure and position, from being relatively multispiral and sinistral

Table 4. Coding scheme for characters used to generate Table 5.

Character No.	Coding
1	0 = absent; 1 = present
2	0 = external; 1 = internal beneath mantle
3	1 = calcified; 2 = without calcification
4	0 = smooth; 1 = rough or lamellate
5	1 = incomplete; 2 = intermediate suspensor present; 3 = complete
6	0 = circular; 1 = rectangular
7	0 = conical; 1 = flattened
8	1 = auriculate; 2 = spatulate
9	1 = anterior; 2 = central; 3 = posterior
10	1 = large; 2 = medium; 3 = small
11	1 = same size; 2 = mantle larger than shell
12	1 = smooth; 2 = pustulose; 3 = puckered
13	0 = absent; 1 = present
14	1 = entire; 2 = weakly emarginate; 3 = deeply cleft
15	0 = entire; 1 = permanently cleft
16	1 = entire; 2 = slightly crenulate; 3 = deeply crenulate
17	1 = absent; 2 = present
18	0 = absent; 1 = present
19	0 = absent; 1 = present
20	0 = one pair; 1 = two pairs
21	0 = separate; 1 = joined
22	1 = very narrow; 2 = narrow; 3 = moderately broad; 4 = very broad
23	0 = absent; 1 = present
24	1 = separated; 2 = together but without basal fusion; 3 = together plus basal fusion
25	0 = absent; 1 = present
26	0 = smooth; 1 = pustulose
27	0 = absent; 1 = present
28	0 = relatively small; 1 = relatively large
29	1 = absent; 2 = present
30	0 = absent; 1 = present
31	1 = well back posterior right; 2 = posterior right; 3 = extending from left corner continuously to posterior midline
32	1 = half length; 2 = less than half length; 3 = almost entire length
33	1 = smooth; 2 = pustulose
34	1 = middle of basement membrane; 2 = in front of hind end of basement membrane; 3 = above hind end; 4 = well behind gill
35	0 = absent; 1 = present
36	0 = mouth not in pedal cleft; 1 = mouth within pedal cleft
37	0 = non-protrusible; 1 = protrusible
38	0 = gland absent; 1 = present
39	1 = absent; 2 = present
40	1 = denticle absent; 2 = present
41	0 = accessory denticle absent; 1 = present
42	0 = lamellae absent; 1 = present
43	0 = cuticularized labial ring; 1 = two separate jaws
44	0 = cruciform; 1 = polygonal
45	1 = smooth; 2 = denticulate
46	1 = monaulic; 2 = diaulic; 3 = triaulic
47	0 = flaps absent; 1 = present
48	0 = absent; 1 = present

Table 4. (continued)

Character No.	Coding
49	1 = anterior midline; 2 = base of right oral tentacle; 3 = on front of gill on right side
50	0 = non-protrusible; 1 = protrusible
51	1 = smooth; 2 = papillose
52	1 = one; 2 = two
53	0 = high; 1 = low
54	1 = absent; 2 = surrounding male duct; 3 = distinct gland
55	1 = gland absent; 2 = present
56	0 = absent; 1 = present
57	0 = vas deferens does not coil within penial sac; 1 = vas deferens coils within penial sac

in Umbraculacea to paucispiral and dextral in Pleurobranchacea is not as great as it might appear. Cox (1960) has demonstrated that all possible states (from hyperstrophic conispiral through planispiral to orthostrophic conispiral) exist in Recent species of the primitive pulmonate family Ampullariidae.

Shells of adult umbraculaceans are covered externally with a tough, adherent periostracum that presumably inhibits encrustation by marine fouling organisms. When, in *Umbraculum*, the periostracum erodes off the apex, the shell is rapidly colonized by algae, barnacles and serpulid polychaetes that spread over its surface (e.g. Bertozzi, 1983, front cover). Only *Umbraculum* calcifies its shell to any degree. There is a progression in shell musculature, as evidenced by muscle scars on the shell's ventral surface, within the Umbraculacea. *Anidolyta* possesses an incomplete circle of muscle attachments where the dorso-ventral and columellar muscles insert onto the shell; *Tyrodina* has a new muscle (intermediate suspensor) in the gap, but the ring of muscles remains incomplete; *Umbraculum* has a complete ring of muscles. I interpret this progression as an ordered series, and have analyzed it as an ordered multistate character.

The mantle cavity has quite disappeared in the Pleurobranchacea. One finds a delicate shell in a shell cavity beneath the mantle in some species of this suborder. The shape of the shell in pleurobranchs is either auriculate (= haliotiform) or spatulate (= triangular). Generally shells of the former shape are relatively large (i.e. they cover the entire visceral cavity) and spatulate shells are small (i.e. they are only one-half to one-fifth the length of the visceral cavity) by contrast. Shell size appears not to be correlated with adult size. The shell is most often located centrally beneath the mantle but there is a tendency for an anterior location in shells of the smaller, spatulate type. All pleurobranch shells are light with meagre calcification and one genus, *Bathyberthella*, is unique because its shell lacks calcification. Sculpture on the shell consists of feeble, concentric growth striae beneath which is a microsculpture of radial punctations or undulating grooves. The shell is never wholly, or even partially, uncovered by the mantle in any pleurobranch when alive (Willan,

**Table 5.** Character state distribution amongst the genera of the Notaspidea (See Tables 3 and 4 for character names and coding system respectively; \* = inapplicable character).

Character No.	<i>Tylocina</i>	<i>Anidolyta</i>	<i>Umbraculum</i>	<i>Berthella</i>	<i>Pleurobranchus</i>	<i>Berthelina</i>	<i>Pleurehdera</i>	<i>Bathyberthella</i>	<i>Pleurobranchella</i>	<i>Pleurobranchaea</i>	<i>Euselenops</i>
1	1	1	1	1	1	1	1	1	0	0	0
2	0	0	0	1	1	1	1	1	*	*	*
3	2	2	2	2	(1,2)	2	2	1	*	*	*
4	0	1	1	0	0	0	0	0	*	*	*
5	2	1	3	1	1	1	1	1	*	*	*
6	0	0	0	1	1	1	1	1	*	*	*
7	0	0	1	*	*	*	*	*	*	*	*
8	*	*	*	1	1	(1,2)	1	1	*	*	*
9	2	2	2	2	(2,3)	1	1	2	*	*	*
10	1	1	2	(1,2)	(1,3)	3	2	1	*	*	*
11	1	1	1	(1,2)	(1,2)	2	2	1	*	*	*
12	1	1	1	1	3	1	1	1	2	2	1
13	0	0	0	1	1	1	*	0	0	0	0
14	1	1	1	2	3	(1,2)	1	1	*	*	*
15	0	0	0	0	0	0	0	0	0	0	1
16	1	2	3	1	1	1	1	1	1	1	1
17	1	1	1	(1,2)	1	1	1	1	1	1	1
18	0	0	0	0	0	0	0	0	1	1	1
19	0	0	0	0	0	0	0	0	0	1	0
20	0	0	1	0	0	0	0	0	0	0	0
21	1	1	0	1	1	1	1	1	1	1	1
22	1	1	*	2	2	2	2	2	3	3	4
23	0	0	*	0	0	0	0	0	1	1	1
24	1	1	2	3	3	3	3	3	1	1	1
25	0	0	0	0	1	0	0	0	0	0	0
26	0	0	1	0	0	0	0	0	0	0	0
27	0	0	0	1	1	0	1	1	0	1	1
28	*	*	*	0	0	*	1	0	*	0	0
29	1	1	1	1	1	1	1	1	1	(1,2)	1
30	0	0	1	0	0	0	0	0	0	0	0
31	1	1	3	2	2	2	2	2	2	2	2
32	1	1	3	2	2	2	2	2	2	2	2
33	1	1	1	1	2	1	1	1	(1,2)	1	2
34	3	3	4	(1,3)	3	3	3	3	2	2	2
35	0	0	1	0	0	0	0	0	0	0	0
36	0	0	1	0	0	0	0	0	0	0	0
37	1	1	0	1	1	1	1	1	1	1	1
38	0	0	0	1	1	1	1	1	1	1	1
39	2	1	1	1	1	1	1	1	(1,2)	2	1
40	2	1	1	(1,2)	(1,2)	1	2	1	1	1	1
41	0	0	0	0	0	0	0	0	0	1	0
42	0	1	0	0	0	1	1	0	0	0	0
43	0	0	0	1	1	1	1	1	1	1	1
44	*	*	*	0	0	0	0	1	1	1	1
45	*	*	*	(1,2)	2	(1,2)	2	2	2	2	1
46	1	2	*	3	2	3	3	3	2	2	2
47	0	0	*	0	1	0	0	0	0	0	0
48	1	1	1	0	0	0	0	0	0	0	0
49	2	2	1	3	3	3	3	3	3	3	3
50	0	0	*	1	1	1	1	1	1	1	1
51	1	1	1	1	1	1	1	1	(1,2)	1	2
52	1	1	*	(1,2)	(1,2)	2	2	2	1	1	1
53	*	*	*	0	0	1	0	0	*	*	1
54	2	2	3	(1,2)	(1,3)	2	2	2	3	3	1
55	1	1	1	2	1	2	2	(1,2)	1	1	1
56	0	0	0	0	0	0	0	0	1	1	0
57	0	0	0	0	0	0	0	0	1	1	0

1978). It is not uncommon to find individuals of normally-shelled species without a shell. Adults of the genera *Pleurobranchaea*, *Pleurobranchella* and *Euselenops* lack shells, but Mr. R. Burn has informed me he discovered a tiny shell in a small juvenile *Pleurobranchaea maculata* he was examining. So, absence of a shell in these three genera is interpreted as an evolutionary loss; this synapomorphy for these three genera is homeoplasious to occasional shell absence in individuals of other pleurobranch genera.

## MANTLE

The mantle of umbraculaceans is thin and unremarkable except for *Umbraculum* where its margins are deeply serrate all round. The mantle attains greater morphological diversity in the Pleurobranchidae following its emancipation from the shell; there is a multiplicity of colors (yellow, red, brown, purple) and patterns of boldly contrasting spots. The larger species have tougher mantles and they often possess elaborate, tuberculate ornamentation. These colors, patterns and ornamentations are species-specific. Glands are present within or below the mantle's epithelium (Marbach and Tsurumal, 1973; histological review by Thompson and Colman, 1984) and small, sub-epithelial spicules occur in the mantles of at least some (probably most) species of *Berthella*, *Pleurobranchus* and *Berthellina*. The anterior margin of the mantle is usually straight or weakly embayed and it permits extension of the oral veil and rhinophoral tips beyond; it is deeply cleft anteriorly in *Pleurobranchus* and *Berthella* (some species). Some species of *Pleurobranchus* raise the posterior section of the mantle behind the gill (e.g. *P. membranaceus*, Thompson and Slinn, 1959; *P. forsskali*, Thompson, 1970) to allow temporary egress of the respiratory current, but only in *Euselenops* is there a permanent mid-posterior mantle crenulation for this purpose. The mantle of pleurobranchs usually covers the foot entirely (this is certainly the case at rest), or the tail may just appear beneath the mantle in an active animal. (Figs. 17 and 18 illustrate exactly how the mantle/foot relations can alter. The two photographs of the same 48 mm long *Pleurobranchus peronii* were taken in the laboratory less than five minutes apart; the first shows the individual at rest and the second shows it crawling actively.) There are, however, at least two exceptions, *Euselenops luniceps* (where the mantle is a little disc barely half the size of the foot) and *Bathyberthella antarctica* (where the foot extends a considerable distance behind the mantle at all times).

The principal apomorphy exhibited by the subfamily Pleurobranchaeinae is fusion of the mantle with the underlying body. Initial fusion occurs anteriorly between the mantle and head causing the separation of, and consequent lateral displacement for, the rhinophores; this condition is possessed by all species of all the pleurobranchaeine genera. Subsequent fusion takes place posteriorly between the mantle and foot, but this fusion is restricted to a small area; this condition occurs only in some species of *Pleurobranchaea*. Fusion, therefore, takes place in a different sequence in the Notaspidea to that of cladobranch nudibranchs (i.e. members of the superfamilies Dendronotoidea, Arminoidea and

Aeolidioidea) where it is first anterior then lateral. Lateral fusion of the mantle and foot (at least on the right side) is obviously impossible in the Notaspidea because of the presence of the gill.

One further consequence of the mantle's emancipation from the shell is increased behavioral versatility. Most pleurobranchs wrap the margins of the mantle around the foot like a cloak when disturbed or lifted off the substratum. Mantle autotomy is known to occur in two species of *Berthella*. *B. kaniae* can cast off irregular pieces of its mantle when provoked (Sphon, 1972), and, when autotomy occurs in *B. martensi*, it always takes place along "preformed shear zones" (Willan, 1984b).

## FOOT

*Umbraculum* possesses a number of unique features related to its foot. This organ is enormous, tough, entirely covered with pustules and it has a very deep, mid-anterior cleft in which the mouth is located. In the Pleurobranchidae, the foot bears a transverse groove anteriorly (see Fig. 18).

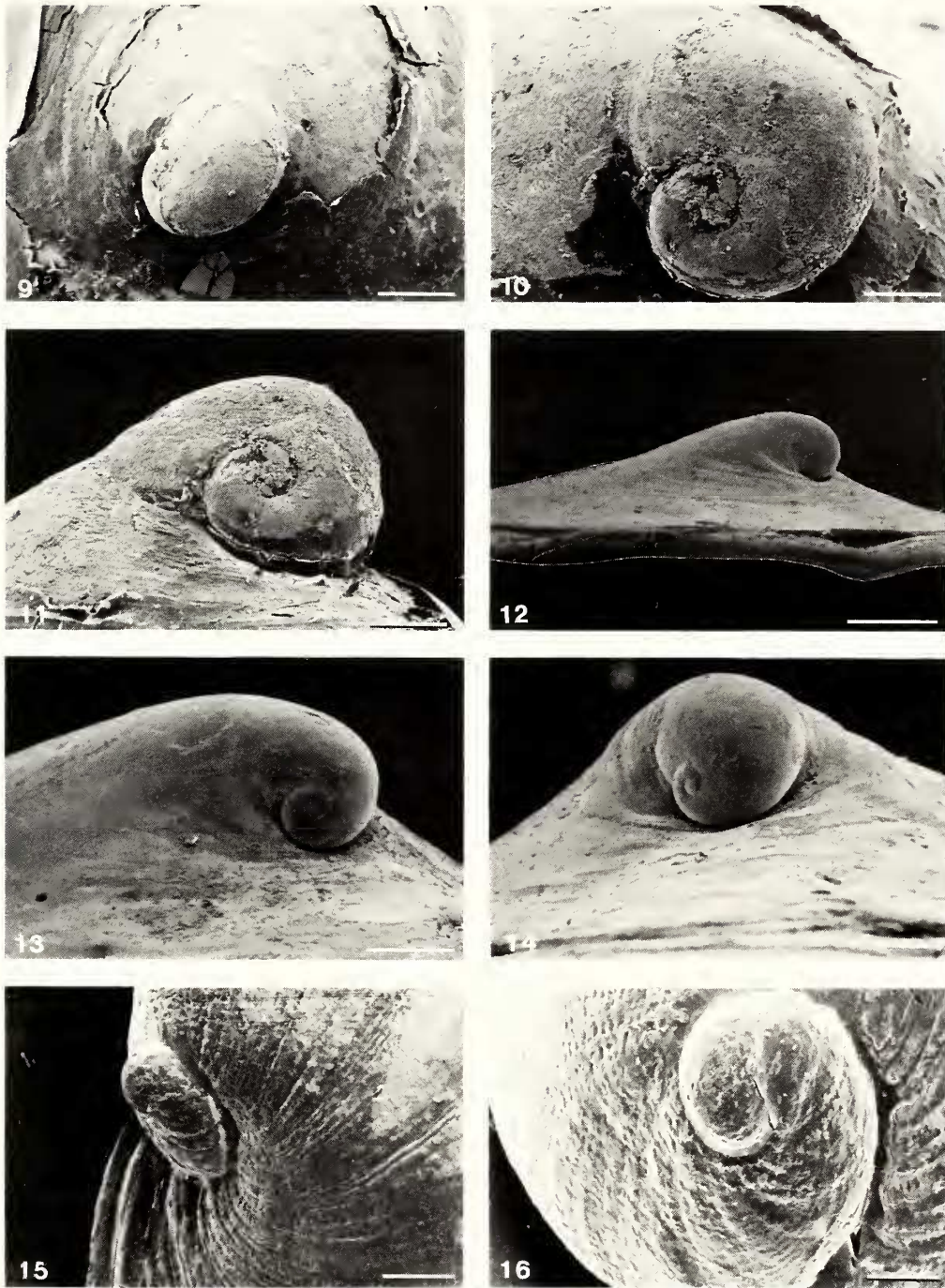
At the rear, a gland is located on the foot sole in all pleurobranch genera except *Berthellina* and *Pleurobranchella*. This pedal gland is shown in Figure 19. It becomes apparent at sexual maturity and probably secretes chemicals for species-specific recognition (Thompson and Slinn, 1959; Macnae, 1962; Willan, 1983). Its occurrence in so many pleurobranch genera would indicate it is a plesiomorphic character, and furthermore, its loss in *Berthellina* and *Pleurobranchella* is not only independent but also secondary. *Pleurobranchus membranaceus*, alone in the order possess the ability to swim by means of its foot; it uses an alternating, flapping movement of the sides of the enlarged foot to propel itself, upside-down, through the water (Thompson and Slinn, 1959).

## GILL

The obvious homologies of the respiratory organ in the Notaspidea, in terms of position, external morphology and direction of blood flow within, present a strong argument for uniting all living side-gilled sea slugs (i.e. notaspideans) within the one order and believing the group to be holophyletic. The terminology of the gill was stabilized by Willan (1983). The central axis of the gill, which lies longitudinally with respect to the body, is the rachis. Side leaves (pinnae), that decrease progressively in size, arise alternately from the rachis and each bears a regular series of fine secondary leaflets (pinnules). The pinnae are symmetric in size between the upper and lower sides of the gill in the Pleurobranchacea and asymmetric in the Umbraculacea.

Thompson and Slinn (1959) and Morton (1972) have shown that ciliary currents direct water between the pinnules. The ciliary currents beat towards the tips of the pinnae. Thompson and Slinn (1959) showed transverse currents across the pinnules whilst Morton (1972) demonstrated downward-directed vertical currents moving fine waste particles between each pinnule and transverse currents at the top and base of each pinna. Within the gill, the efferent branchial vessel runs along the exposed lateral edge and the





**Figs. 9-16.** Scanning electron micrographs of protoconchs of notaspidean shells. **Fig. 9.** *Tylodina corticalis* (Tate): dorsal view; specimen from 18 m, Julian Rocks, east of Cape Byron, northern New South Wales, Australia; 23° tilt; bar = 200  $\mu\text{m}$ . **Fig. 10.** *T. corticalis*: view from top left showing detail of sinistral coiling; same specimen as in Fig. 9; 47° tilt; bar = 100  $\mu\text{m}$ . **Fig. 11.** *T. corticalis*: left profile; same specimen as in Fig. 9; 84° tilt; bar = 100  $\mu\text{m}$ . **Fig. 12.** *Umbraculum umbraculum* (Lightfoot): left profile showing protoconch and teleoconch of juvenile shell; specimen from Byron Bay, northern New South Wales, Australia (Australian Museum, Sydney, Reg. No. C5279); 90° tilt; bar = 1 mm. **Fig. 13.** *U. umbraculum*: left profile showing detail of sinistral coiling; specimen from Port Jackson, New South Wales, Australia (Museum of Victoria, Reg. No. F11424); 91° tilt; bar = 400  $\mu\text{m}$ . **Fig. 14.** *U. umbraculum*: view from the rear, same specimen as in Fig. 12; 90° tilt; bar = 400  $\mu\text{m}$ . **Fig. 15.** *Berthella pellucida* (Pease): dorsal view showing profile of protoconch; specimen from intertidal reef, Moreton Bay, southern Queensland; 0° tilt; bar = 200  $\mu\text{m}$ . **Fig. 16.** *B. pellucida*: view from posterior right showing detail of dextral coiling; same specimen as in Fig. 15; 45° tilt; bar = 200  $\mu\text{m}$ .



**Figs. 17 and 18.** Mantle/foot relationships of living *Pleurobranchus peronii* Cuvier. Both photographs depict the same individual (note scar on mantle behind left rhinophore) and were taken less than five minutes apart. Figure 17 shows the animal at rest and figure 18 shows it crawling actively. Specimen (48 mm extended crawling length) from an intertidal pool, Hastings Point, northern New South Wales, Australia, August 1984. Photographs by R. C. Willan.

afferent vessel runs on the mesial edge closest to the body wall (Moquin-Tandon, 1870; Thompson and Slinn, 1959; Morton, 1972). Blood flows within the pinnules in upwards-directed vertical vessels; as many vessels being present as there are pinnules. The rachal tubercles, besides producing mucus, act as "guides" for fine particles, each leading material off the rachis onto the pinna that arises next to it.

The gill is attached to the lateral body wall by two contiguous suspensory membranes. In *Tylodina* and *Anidolyta*, only the anterior half of the gill is attached. Throughout the Pleurobranchidae, the gill is attached for more than half its length. In *Umbraculum*, the gill is attached for almost its entire length. The gill of *Umbraculum* extends from a mid-anterior point on the body in a continuous crescent, around the right side, well back into the right posterior quadrant. Such a situation of extreme branchial enlargement is most unusual and it appears to be another manifestation of the bodily reorganization undergone by *Umbraculum*; one probably necessitated by presence of the flattened, inflexible shell and tough, enlarged foot. The free posterior part of the gill is muscular and mobile in all pleurobranchs (Thompson and Slinn, 1959).

The gill rachis of the Notaspidea is primitively smooth but it bears a series of tubercles in some genera (for example *Pleurobranchus*, see Fig. 19). A tubercle is present on the outer face of the rachis at the point a pinna arises laterally. That tubercles occur on the gill rachis in the otherwise not closely related genera *Pleurobranchus* (where their presence is correlated with the development of tubercles on the mantle) and *Euselenops* (where the mantle is smooth) demonstrates a case of convergent apomorphy. In *Pleurobranchella*, the gill rachis can apparently be smooth or weakly tuberculate depending on the species; however, in the species that do possess them, the tubercles are unlike those of *Euselenops* or *Pleurobranchus*, being merely a series of swellings that are separated by narrow, vertical, somewhat undulating grooves (pers. obs.).



**Fig. 19.** Pedal gland on posterior foot sole of a living *Pleurobranchus peronii* Cuvier. Note tubercles on gill rachis between mantle and foot. Specimen (86 mm extended crawling length) from an intertidal pool, Hastings Point, northern New South Wales, Australia, February 1984. Photograph by R. C. Willan.

## ORAL TENTACLES

In all notaspidean genera bar *Umbraculum*, the oral tentacles and rhinophores possess longitudinal grooves. In all genera but *Umbraculum* again, the oral tentacles are connected to each other by a flap of tissue, the oral veil, that joins them. This veil overhangs the mouth and presumably increases the area sensitive to tactile stimuli and, in fact, all species of *Pleurobranchella*, *Pleurobranchaea* and *Euselenops* have further enlarged the surface area for touch reception by elaborating compound papillae along the anterior margin of the oral veil. In life, pleurobranchs ripple the oral veil over the surface in an exploratory manner as the animal crawls (Willan, 1983). *Pleurobranchaea* also uses its oral veil to surround and hold prey (Willan, 1984a). The oral veil develops

by anterior extension of, and fusion between, the oral tentacles during ontogeny (Usuki, 1969). This oral veil can only be interpreted as one of the symplesiomorphies of the Notaspidea because of its presence throughout the entire order (except *Umbraculum*), even in the most primitive genera *Tylodina* and *Anidolyta*. *Umbraculum* has a remarkable set of oral tentacles that are completely different to any other side-gilled sea slug. It has two pairs of pincer-like oral tentacles at the very base of its muscular foot.

The rhinophores of *Umbraculum* are located side-by-side anteriorly in the midline. This position of the rhinophores represents the symplesiomorphic state too for the Pleurobranchidae and there, it is accompanied by fusion of the basal third of the organs so that they arise from a common base. However in the more advanced Pleurobranchaeinae, the rhinophores are widely separated at the sides of the head because of the ontogenetic fusion of mantle and head to yield confluence of mantle and oral veil. This condition of rhinophoral separation is unquestionably an apomorphy of this pleurobranchaeine group and one would need to follow its ontogeny to determine whether its present condition came about by way of an ancestor like *Tylodina* (where the rhinophores are initially separate during development) or if it was secondary and arose from a pleurobranchine ancestor with closely-positioned rhinophores. Among the Pleurobranchidae, the rhinophores of members of the genus *Pleurobranchus* are noteworthy in that, in living specimens, their tips pulsate regularly; the more active the animal, the faster and more vigorous the pulsations.

## GUT

Two regions of the gut present important characters that enable discrimination between taxa. These are the foregut (the pharyngeal bulb in particular) and the hindgut. The parts of major importance are the radula, jaws, median buccal gland and anus.

All members of the Notaspidae have a multiseriate, ptenoglossan radula with numerous rows of (generally) undifferentiated teeth precisely like that suggested for early opisthobranchs (Morton, 1955). A central (or rachidian) tooth is present only in *Tylodina* among the Umbraculacea, and *Pleurobranchaea* and *Pleurobranchella* (some species) among the Pleurobranchacea. Its absence throughout the pleurobranchine genera must therefore, be considered a symplesiomorphy of long standing. The teeth across any particular row are generally similar to each other, although they may differ in size (middle laterals tend to be relatively larger than inner or outer laterals) and shape (inner and middle laterals are broader, whereas outer laterals are narrower and more elongate). Ontogenetic variation within notaspidean radulae parallels that of anthobranch nudibranchs (Bertsch, 1976).

Notaspideans show a widespread tendency to develop secondary denticles on the blade below the cusp of a radular tooth. The position and number of these denticles varies between genera: *Tylodina* bears a single denticle at the base of the main cusp; *Anidolyta* has two or three denticles equally arranged between the cusp and base; *Berthellina* has a row of many (2 to 15) denticles along the distal half of the

tooth; *Pleurehdera* has a single denticle located close to the base on inner lateral teeth and it appears in a more and more distal location on progressive outer lateral teeth, at the same time decreasing in height; *Pleurobranchaea* has one (either strong or rudimentary) denticle arising from the base of the cusp. *Umbraculum*, *Berthella*, *Pleurobranchus*, *Bathyberthella*, *Pleurobranchella* and *Euselenops* never bear secondary denticles (although a small denticle does occur at the base of the tooth in one species of *Pleurobranchus*, *P. membranaceus*). This diversity of locations and configurations of secondary denticles through the taxa suggests that the Notaspidea primitively had simple, smooth teeth (as in *Umbraculum*) and denticles were acquired later independently in the various lineages, probably concordantly with tooth elongation, to improve feeding efficiency. Certainly the genus with the longest teeth (*Berthellina*) is the one that has the most denticles. I do not think diet canalized tooth structure because, although there are many sponge-rasping notaspideans (i.e. the genera *Umbraculum*, *Tylodina*, *Anidolyta*, *Berthella* and *Berthellina*), there exists a multiplicity of tooth shapes between these genera.

The structure of the labial cuticle presents one of the strongest pieces of evidence in support of a major dictotomy between the two notaspidean suborders. In the Umbraculacea, there is a (variably thickened) cuticularized ring lining the pharyngeal bulb. In the Pleurobranchacea, by contrast, two patches of specialized cuticle (jaws) are present. The jaws are composed of numerous rodlets with flattened, interlocking plates on their inner face. MacFarland (1966, p. 96, 97) has thoroughly described the formation and growth of these mandibular elements, each from a single, large, cuboidal rhabdoplast. These jaws, composed of stacked rodlets, are probably more primitive than the cuticularized ring; Gosliner (1981) envisages the hypothetical opisthobranch ancestor as possessing two well developed jaws. Differences occur between the two subfamilies regarding the shape of the mandibular elements at the jaw's surface; those of the Pleurobranchaeinae are oval or polygonal, whilst those of (most of) the Pleurobranchinae are cruciform with interlocking lateral projections. *Bathyberthella* presents the sole exception to the latter rule; its mandibular elements lack lateral projections and look like those of *Pleurobranchaea* in surface view (Willan, 1983, Figs. 50-53; Willan and Bertsch, 1987, Fig. 6 a-d). I initially suggested that the form of the mandibular elements in *Bathyberthella* might be an example of a retained plesiomorphy linking this genus to the Pleurobranchaeinae, but discovery of a second species in the genus forced a reinterpretation of that view (Willan and Bertsch, 1987). The mandibular elements of *Bathyberthella* must now be viewed as a case of convergence. The anterior margin of oval or polygonal elements (or its homologue, the blade, in cruciform elements) is usually denticulate. This is apparently the case in all genera except *Berthella*, *Berthellina* and *Pleurehdera* where the blade is smooth. However it is precisely these three genera that show greatest intraspecific and intra-individual variation in this character (Willan, 1984b), so no phylogenetic deductions can be made. Nor, for the reasons of this variability just cited, should taxonomic judgements be based solely

on the structure of the mandibular elements. I have already suggested the oval type of mandibular element with denticulate anterior border preceded the cruciform type (Willan, 1983).

The epithelium that lines the anterior section of the stomach ("gizzard") of *Tylodina* has a strong cuticular layer that bears irregular, cuticularized papillae arranged in rows (Vayssière, 1883; Pelseneer, 1894, MacFarland, 1966).

One apomorphic organ possessed by all members of the Pleurobranchidae is a median buccal (= acid or dorsal accessory) gland. The duct of this gland enters the pharyngeal bulb anteriorly on the mid-dorsal surface. The median duct is long and tubular and it branches into a network of fine tubules distally. The tubules are best developed in *Pleurobranchaea* where they can be seen as soon as the body cavity is opened; they ramify extensively between, and are loosely connected to, the viscera (Willan, 1975; Morse, 1984). These tubules are hollow and their tips possess numerous, thin walled, vacuolated cells surrounded by delicate, muscle slips. The cells secrete a highly acidic fluid (pH = 1 to 1.2) which is apparently propelled along the ducts by the muscles and stored in the spongy median duct (Thompson and Slinn, 1959; Thompson and Colman, 1984; Morse, 1984). This duct is extraordinarily long in *Bathyberthella*; in *B. antarctica* it measures about twice the animal's crawling length when fully unravelled (Willan and Bertsch, 1987).

The usual site of debouchement for the anus is just above the posterior end of the gill's suspensory membrane, and this site is presumed to be primitive. However, certain notaspideans have the anal opening in advance of, or behind, this site. The anus opens a short distance in front of the hind end of the basement membrane in all species of the genera *Pleurobranchella*, *Pleurobranchaea* and *Euselenops*. A minority (about three) of species of *Berthella* have the anal opening directly above the gill within the anterior half of the basement membrane. These genera show no development of an anal tube to direct faeces off the gill. In *Umbraculum* the anus opens on an anal tube, an obvious apomorphy, well behind the rear end of the basement membrane.

## REPRODUCTIVE SYSTEM

The Notaspidea possesses a variety of reproductive configurations that encompass all three major evolutionary grades, monaulic, diallic and triaulic. The monaulic condition seen in *Tylodina* is very primitive. Not only is there a simple, straight-through gonoduct (with only the coelomic section being elaborated into an ampulla), but there is also a non-protrusible cephalic penis bearing an external ciliated groove. *Tylodina* possesses a single allosperm receptacle (i.e. bursa copulatrix) with its opening to the exterior contiguous to that of the undivided pallial gonoduct (MacFarland, 1966). Gosliner (1981) also recognized a second minute allosperm receptacle (i.e. receptaculum seminis) arising off the pallial gonoduct at the point of entry into the nidamental glands. Thus the reproductive system of *Tylodina* "remains essentially unmodified from the hypothetical ancestral (opisthobranch) condition" (Gosliner, 1981).

All remaining notaspidean taxa show (partial or com-

plete) separation of the pallial gonoduct.

All who have studied the reproductive system of *Umbraculum* report a very unusual configuration (Moquin-Tandon, 1870; Ev. Marcus and Er. Marcus, 1967; Ev. Marcus, 1985). The system does need reinvestigating to interpret the homologies of the organs with those of other opisthobranchs and it also needs analysing physiologically to follow the pathways of sperm and eggs as Thompson and Bebbington (1969) have done so thoroughly for *Aplysia*. *Umbraculum* has its pallial gonoduct divided by an inner, longitudinal fold into seminal and oviducal efferent channels with a prostate gland associated with the former (Ev. Marcus and Er. Marcus, 1967). There are two allosperm receptacles in *Umbraculum*. *Umbraculum*, like *Tylodina* and *Anidolyta*, has an external penis with ciliated groove (Ev. Marcus and Er. Marcus, 1967). Pruvot-Fol's (1960) belief that the penis (as here designated) of *Umbraculum* was no more than an elaborate genital flap (as in *Pleurobranchus*) from which emerged, terminally, a filiform "true" penis, has not been authenticated. Hartley (1964) has given a brief account of oviposition and early development in *Umbraculum*.

The genera of the Pleurobranchidae fall into two groups depending on the configuration of their reproductive systems. In both groups the reproductive systems are complicated, but this complexity is manifest in different ways. All members of the first group (*Pleurobranchella*, *Pleurobranchaea*, *Euselenops*) are diallic; all have isolated the nidamental glands, reduced the number of allosperm receptacles to one (the bursa copulatrix) and elaborated the terminal male genitalia. In *Pleurobranchella* and *Pleurobranchaea*, the distal vas deferens is greatly elongated and its coils are stowed in a penial sac, an extension of the muscular penial sheath. In both, a distinct, lobed prostate gland is present. All genera of the second group (*Berthella*, *Berthellina*, *Bathyberthella*, *Pleurehdera* and *Pleurobranchus*) have acquired a condition of triauly within their reproductive systems. In all but *Pleurobranchus*, a separate oviduct runs through the nidamental glands. Several other significant features accompany the triaulic condition in genera of this group. Among them are apomorphies like ensheathment of the vas deferens by the prostate gland, absence of an anatomically distinct prostate, acquisition of a penial gland. (This gland, sometimes termed an accessory prostate, is a conspicuous and tubular organ arising from the distal section of the vas deferens close to the penis.) There is also the plesiomorphic persistence of two allosperm receptacles, one of which (the receptaculum seminis) arises high up off the duct of the bursa copulatrix. In the genus *Berthellina*, the receptaculum seminis branches off the vagina high up near the bursa copulatrix; not at the plesiomorphic site close to the vaginal aperture. *Pleurobranchus*, whilst obviously part of this triaulic group, has several apomorphies of its reproductive system. First is the elaboration of the skin surrounding the genital apertures of adult animals into large flaps that presumably function to assist copulation. Second is the reduction, in a few species (previously classified as *Oscanius*), of the number of allosperm receptacles to one (bursa copulatrix). Third is the absence of a penial gland. This gland is also ab-

sent in one species of *Bathyberthella* (*B. antarctica*), but because all other species and genera close to *Bathyberthella* possess penial glands I interpret its absence in this particular species to be the result of evolutionary loss instead of primary absence. It is presumed that, in *B. antarctica*, a section of the considerably enlarged prostate gland has taken over the function of the penial gland (Willan and Bertsch, 1987).

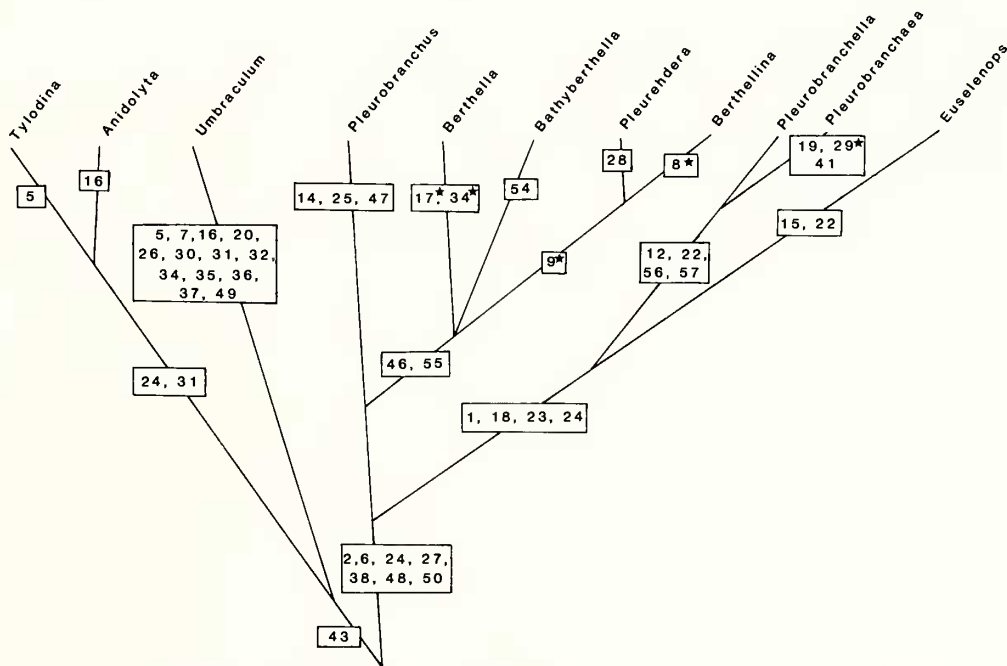
In contrast to the conservatism of penial structure in members of the Pleurobranchinae, the subfamily Pleurobranchaeinae shows a surprising structural diversity. Some species (of *Pleurobranchaea*) do possess the plesiomorphic smooth penis that lacks any cuticular thickenings. Other species of *Pleurobranchaea* apparently possess either an external cuticle or internal stylet (Ev. Marcus and Gosliner, 1984). Gosliner (1985) claimed that, for the genus *Pleurobranchaea*, penial morphology is species-specific, and no significant change occurs with growth or state of maturity. This contradicts MacFarland's (1966) earlier observations on *P. californica*. A developmental sequence urgently needs to be investigated to substantiate these assertions. Papillae are present on the outside of the penis of *Pleurobranchella* (only sparsely developed) and *Euselenops* (copiously developed).

### PHYLOGENETIC HYPOTHESIS

Figure 20 is a cladogram showing inferred phylogenetic relationships amongst the genera of the Notaspidea. Internal nodes (branching points) represent hypothetical ancestors and external nodes (branch tips) in-

dicate extant genera. Numbers besides branches correspond to the characters given in Table 3 and indicate apomorphies (both autapomorphies and synapomorphies) for that particular branch. Where a branch shows an apomorphic trait for a particular character (i.e. it is not possessed by all species), that character is marked with an asterisk. Characters occurring independently in separate lineages (homeoplasies) are not indicated on this cladogram. No attempt has been made to estimate the amount of morphological evolution between taxa, so branch lengths are not proportional to each other.

The Wagner Tree method, on which this analysis is based, hypothesizes a basal separation of the Notaspidea into two phylogenetic lineages that correspond in membership to the established suborders Umbraculacea and Pleurobranchacea. Within the former, *Umbraculum* is separated as a sister group to *Tyrodina* and *Anidolyta*. Within the latter suborder [sometimes termed the "higher" Notaspidea (Minichev, 1970)], seven discrete apomorphies argue strongly in favour of the belief of monophyly for the Pleurobranchacea. Here, two major subgroups can be discerned; one consisting of the genera *Pleurobranchus*, *Berthella*, *Bathyberthella*, *Pleurehdera* and *Berthellina*; the other consisting of *Pleurobranchella*, *Pleurobranchaea* and *Euselenops*. *Pleurobranchus* forms a sister group to the four remaining genera in the former, and there is a trichotomy (i.e. an unresolved dichotomy) necessitated because *Bathyberthella* shares not a single apomorphy (again it is stressed that this statement relates only to characters employed in this study) with either of its sister groups, *Berthella* or *Pleurehdera/Berthellina*. *Euselenops* forms a sister group to the two remaining genera



**Fig. 20.** Cladogram showing phylogenetic hypothesis for relationships between genera of the order Notaspidea. Numbers refer to character transformations listed in Table 3. Asterisks indicate the presence of apomorphic traits (i.e. apomorphies possessed by only some species within that particular genus).

in the latter subgroup.

Strict adherence to the law of parsimony in the construction of this cladogram has necessitated the classification of 12 characters (numbers 4, 10, 11, 12, 21, 33, 34, 40, 42, 51, 53, 54) as homeoplasies. This implies that these characters, which cannot be employed for Hennigian phylogenetic considerations, have been derived independently in different branches of the tree and hence are not unique to any one particular branch. Each of these characters are now explained separately.

**Character 4.** The plesiomorphic state amongst the Notaspidea is to have a thin periostracum that adheres closely to the shell. But in two of the Umbraculacean genera (*Anidolyta* and *Umbraculum*) the periostracum is scale- or beard-like. *Tylodina*, the genus most closely related to these two retains a smooth, adherent periostracum.

**Characters 10 and 11.** The shell has been reduced in size, independently it would appear, in each of the major notaspidean lineages. So presence of a medium- to small-sized shell, as in *Tylodina*, *Umbraculum*, *Berthella* (some species), *Pleurobranchus* (most species), *Berthellina* and *Pleurehdera* does not indicate phylogenetic affinity. It should be noted that both the body to shell ratio (character 10) and body to mantle ratio (character 11) show apomorphic traits in two genera (*Berthella* and *Pleurobranchus*).

**Character 12.** The plesiomorphic state of the mantle throughout the Notaspidea is to be smooth-textured. Yet in three genera (*Pleurobranchus*, *Pleurobranchella* and *Pleurobranchaea*) the mantle is pustulose. That this ornamentation has been derived independently is evident when its structure is examined in detail. The mantle of *Pleurobranchus* has regular, rounded tubercles (mamillae) that are conical or flat-topped; that of the other two genera is irregularly puckered by minute, intersecting ridges or folds.

**Character 21.** The development of a veil anteriorly between the oral tentacles is a derived condition adopted, it would appear, very early on in the evolution of the Notaspidea. Its absence alone in *Umbraculum* might well be secondary (in which case it would be a plesiomorphy for the whole order). At this time I view the moderately extended tissue connection between the base of the oral tentacles (the "buccal shield" of MacFarland, 1966) of *Tylodina* and *Anidolyta* as homologous with the enlarged, sail-like construction that unites the oral tentacles of all pleurobranchs.

**Character 33.** The texture of the outer surface of the gill's rachis in the Pleurobranchinae is correlated with that of the mantle's surface (they are probably under the same genetic controlling mechanism), i.e. *Pleurobranchus* always has a tuberculate rachis and mantle and both are always smooth in all the other genera. However in pleurobranchaeine genera that have irregularly textured mantles (*Pleurobranchella* and *Pleurobranchaea*), the same relationship does not hold. In *Pleurobranchella* the gill rachis is variable (tubercles are present in *P. alba* but not in *P. nicobarica* (pers. obs.), and in the smooth-mantled *Euselelops*, the rachis is tuberculate.

**Character 34.** With the exception of *Umbraculum* (where the posterior anal position is obviously derived), the

Notaspidea mostly have the anus opening at, or close to, the rear of the gill's suspensory membrane. There appears to have been a trend, in the Pleurobranchacea, for the progressive forward movement of the anus. *Berthella* shows apomorphic traits (see the section on character analyses above) and all genera of the subfamily Pleurobranchaeinae have the anus in front of the hind end of the gill. The different anal positions in these two lineages indicate the homeoplasious nature of this character.

**Character 40.** As explained earlier, species from the following genera possess a small denticle at the base of the inner face of, at least some, lateral teeth in their radula: *Tylodina*; *Berthella*; *Pleurobranchus*; *Pleurehdera*. These denticles vary in their precise position and magnitude as could be expected from a homeoplasious character. It is noteworthy that this character is variable between two pairs of closely-related sister genera (i.e. present in *Tylodina* but not *Anidolyta*; present in *Pleurehdera* but not *Berthellina*).

**Character 42.** The plesiomorphic condition amongst the Notaspidea is to have simple radular teeth without additional denticles. However, throughout the order, lineages have independently acquired such structures. The presence of denticles reaches its zenith in *Berthellina* where teeth are greatly elongate and can possess up to 15 denticles on the distal half of their blades. Since similar denticles are present, though fewer in number in *Pleurehdera*, one can assume the character is an autapomorphy for that sister group. Yet, similar denticles are present on the teeth of *Anidolyta* and there they must be regarded as homeoplasious.

**Character 51.** Penial papillae appear to have evolved independently in two genera of the Pleurobranchaeinae, *Pleurobranchella* (shows apomorphic traits) and *Euselelops*. The detailed structure of the penial papillae and their arrangement is not precisely the same in these genera, their presence probably being related to species-specific morphology of the reproductive tract.

**Character 53.** The plesiomorphic position for the receptaculum seminis is low on the vagina near the female genital aperture when two allosperm receptacles are present. The point of origin is located further up the vagina in *Berthellina* and *Euselelops*, an independent shift it would seem.

**Character 54.** The distribution amongst notaspidean genera of character states relating to the prostate gland is confused. Prostatic tissue either ensheaths the male efferent duct or forms a distinct, lobed gland; mutually exclusive conditions it would appear. But the distinction is not so clear cut when individual genera are considered (see Table 4). A prostate gland is apparently absent in *Berthella* (some species), *Pleurobranchus* (some species) and *Euselelops*. It ensheaths the vas deferens in *Tylodina* and *Anidolyta* (in both it is not anatomically distinct), *Berthellina*, *Berthella* (some species), *Pleurehdera* and *Bathyberthella*. It occurs as a distinct gland in *Umbraculum*, *Pleurobranchus* (some species), *Pleurobranchella* and *Pleurobranchaea*. The trend throughout all the lineages then, is towards separation off of the prostatic tissue from the vas deferens to form a distinct gland. This process appears to have occurred independently in all clades but the *Berthella/Bathyberthella/Pleurehdera/Berthellina* one. Some

of the confusion about this character may have arisen through inadequate early descriptions of reproductive systems and histological studies are now required to delineate the extent and relationships of the prostatic section of the male duct.

Apomorphies need not only be specialized characters that a taxon possesses. Apomorphies can be manifested also by losses, and amongst the Notaspidea there are four cases (character numbers 27, 39, 45, 52) where lineages or branch tips have independently lost structures. All four are extremely important in phylogenetic considerations and they are now discussed separately.

**Character 27.** Possession of a pedal gland by sexually mature animals is a symplesiomorphy of the Pleurobranchidae and so its absence in two otherwise distinct genera, *Berthellina* and *Pleurobranchella*, argues for independent loss.

**Character 39.** Most lineages of notaspideans have no central (rachidian) tooth in their radulae. I believe this absence is due to independent loss.

**Character 45.** Earlier in this paper I postulated that the ancestral condition amongst the pleurobranchs was to have denticulate anterior borders (= blades) to the jaw's mandibular elements. In this case, outgroup comparison is impossible because the Umbraculacea lack mandibular elements completely. Therefore I consider the smooth-bladed condition of the mandibular elements as is found in *Berthella* (some species), *Berthellina* (most species) and *Euselenops* to have occurred independently by simplification from the ancestral (denticulate) condition.

**Character 52.** The plesiomorphic condition in the Notaspidea is to possess two allosperm receptacles (bursa copulatrix and receptaculum seminis), however several lineages have independently reduced that number to one by loss of the receptaculum seminis. Loss of the receptaculum has occurred throughout all of the Pleurobranchaeinae whilst in *Tylodina*, *Berthella* and *Pleurobranchus* apomorphic traits for its loss are evident.

One anomalous character (number 44) deserves further note. Apart from *Bathyberthella*, the disposition of character states relating to mandibular elements is straightforward throughout the major lineages, i.e. cruciform in pleurobranchine lineages and polygonal in pleurobranchaeine lineages. *Bathyberthella* is clearly an exception and the significance of its elongate-polygonal mandibular elements, already touched on in a previous section, is discussed further in the forthcoming section on generic evaluation.

## PHENETIC ANALYSIS

The dendrogram resulting from the "TAXON" program is presented in Figure 21. It agrees extremely well with the manually derived phylogenetic cladogram that I have presented earlier in this paper (Fig. 20). The dendrogram clearly distinguishes three clusters of genera in the order corresponding to the taxa Umbraculacea, Pleurobranchinae and Pleurobranchaeinae. Note that this strictly dichotomous program links *Berthella* with *Bathyberthella*. According to this analysis, the two genera with greatest affinity (i.e. most

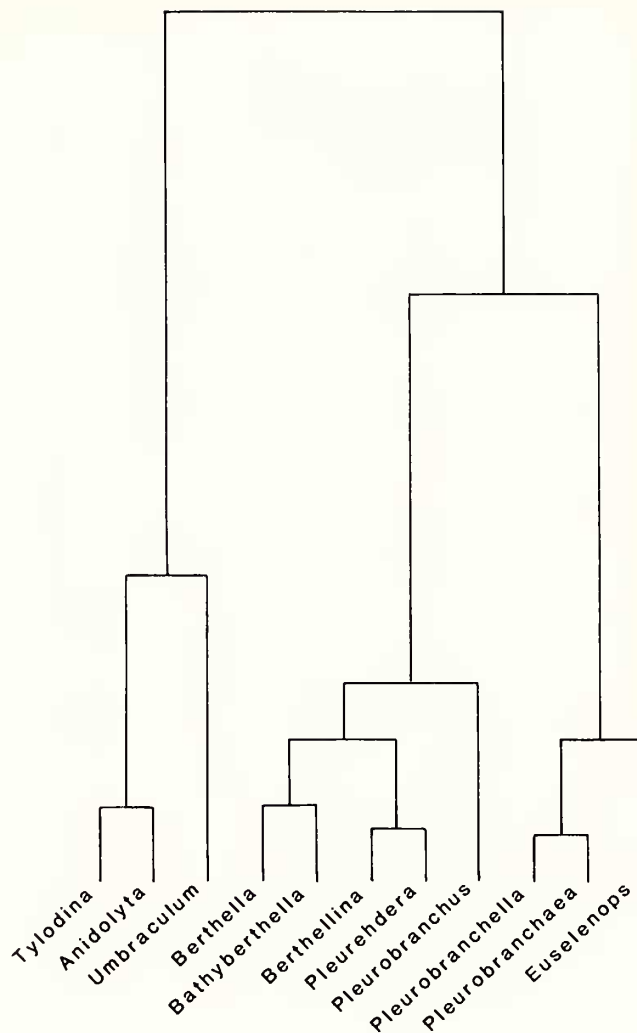


Fig. 21. Phenetic analysis of relationships between genera of the order Notaspidea. Dendrogram results from application of 'TAXON' computer program to data in Table 5.

characters in common) are *Pleurobranchella* and *Pleurobranchaea*.

This "TAXON" program was able to identify the most useful discriminating attributes between groups in the hierarchy. Those singled out for distinguishing between the Umbraculacea (3 members) and Pleurobranchacea (8 members) were shell position, shell shape, oral veil width, gill location, median buccal gland, labial cuticularization, autospermal groove, and penial position. Chief discriminators between the Pleurobranchinae (5 members) and Pleurobranchaeinae (3 members) were shell presence /absence, anterior fusion of mantle and head, oral veil width, papillae on oral veil, relationships of the rhinophores, anal position, mandibular element shape and penial gland. Chief discriminations between the Tylochinidae (2 members) and Umbraculidae (1 member) were shell length to height ratio, shell length to body length ratio, mantle texture, mantle margin, number of pairs of oral tentacles, connection of oral tentacles

by an oral veil, texture of dorsal surface of foot, vertical anterior cleft in foot, anal tube, position of mouth and protrusibility of buccal mass. Attributes discriminating between *Pleurobranchus* and the remaining pleurobranchine genera (4 members) were mantle texture, activity of rhinophoral tips, genital flaps, shape of prostate gland and penial gland. Attributes discriminating *Eusefenops* from the remaining two pleurobranchaeine genera were mantle texture, posterior mantle border, anterior margin of mandibular elements, muscular penial sac, and coiling of the vas deferens. Attributes cleaving the Pleurobranchidae (apart from *Pleurobranchus*) into two groups each containing two genera were shell location, shell length to body length ratio, size of pedal gland, and numbers of denticulate lateral teeth in the radula. Attributes discriminating between the genera *Tyrodina* and *Anidolyta* were nature of periostracum, mantle margin, rachidian teeth and numbers of denticulate lateral teeth in the radula. Attributes discriminating between the genera *Berthella* and *Bathyberthella* were shell calcification, mantle spicules, anterior border of mantle and shape of mandibular elements. Attributes discriminating between the genera *Berthellina* and *Pleurehdera* were shell length to body length ratio, pedal gland and relative position of receptaculum seminis. Finally, the attributes discriminating between the genera *Pleurobranchella* and *Pleurobranchaetae* were posterior mantle/foot fusion, pedal gland and presence of accessory denticles on radular teeth.

The "CRAMER" routine of the "TAXON" program was run to explore possibilities of groupings other than those presented in the dendrogram. That "CRAMER" was largely unsuccessful adds more credibility to the original dendrogram. "CRAMER" did suggest an alternative grouping for *Pleurobranchus*; that genus became allied to the subfamily Pleurobranchaeinae on the grounds of reproductive condition and lack of a penial gland.

## DISCUSSION

### REAPPRAISAL OF FAMILIES

The great similarity between the phylogenetic cladogram (Fig. 20) and phenetic dendrogram (Fig. 21) suggests that, given the character set used here, the hypothesis these analyses supports has a high probability of being the correct one. That this hypothesis has been corroborated is gratifying when one recalls that for any 11 taxa, the possible number of rooted phylogenetic trees with labelled tips and with unlabelled interior nodes is  $6.9 \times 10^9$  (Felsenstein, 1978). Additional support for the basic lineages of this hypothesis has come from recent investigations on notaspidean sperm ultrastructure (Healy and Willan, 1984) and diet (Willan, 1984a).

The evidence (from shell, gut, mantle-gill complex and reproductive system) overwhelmingly points to a monophyletic origin for the Notaspidea. Two Russian workers, Minichev and Starobogatov (1978), proposed a polyphyletic derivation for the group and erected the new orders Umbraculida and Pleurobranchida belonging to the (newly con-

stituted) subclasses Dexterobranchia and Opisthobranchia respectively. Their hypothesis rested entirely on characters of the mantle-gill complex and protoconch. In the following year, these same authors proposed a sweeping reclassification of higher taxa in the Opisthobranchia *sensu* Minichev and Starobogatov in a short paper written in Russian (Minichev and Starobogatov, 1979). This reclassification has only recently been published in English (Minichev and Starobogatov, 1984). It purports to use the reproductive system to support grandiose elevation of taxa; the pleurobranchs are raised to an order (Pleurobranchida) containing three suborders (Pleurobranchina, Berthellina and Berthelleina), the latter two newly named. Nowhere do the authors state the particular genera contained within their suborders and even worse, nowhere do they present or give reference to, the anatomical data on which their systems are based. To indicate the futility of new classifications and taxonomic inflation based on single systems, I will disprove the characters to which Minichev and Starobogatov attributed so much importance by showing them to be false. Minichev and Starobogatov's account of protoconchs is incorrect; those of the Umbraculacea are actually hyperstrophic. Many species of *Berthella* do not possess a connection (a special vaginal duct) between the vagina and oviduct; the condition varies within genera. Finally, similar mantle-gill relationships are also found in the Runcinacea and Thecosomata, so that character is homeoplasious. What is needed now is comparative anatomical data not more higher taxa.

Despite the confusion brought about by unsupported taxonomic inflation, the available data do emphasize the separation of the Notaspidea into two subgroups. This basic separation is evidenced by the great differences in buccal cuticularization, shell morphology, gill location, male efferent canal, penial position, median buccal gland and penial gland. Each group has been traditionally considered as a suborder (i.e. Umbraculacea and Pleurobranchacea), and I think that is still the best taxonomic level to treat them at.

Within the Umbraculacea there is again a major dichotomy; *Tyrodina* and *Anidolyta* being fused together to one side and *Umbraculum* to the other. As I will expand on the genus *Umbraculum* in the subsequent section, there is no need to outline here the very many specialized, derived characters possessed by that genus and (monotypic) family. Suffice to say that the Umbraculidae well merits separation, at the family level, from its sister tylodinid group. This is the more generally accepted position in the literature (e.g. Pruvot-Fol and Fischer-Piette, 1934; Pruvot-Fol, 1954; Burn, 1962; Thompson, 1970; Odhner in Grassé, 1968; Rehder, 1980; Bertsch, 1980; Ev. Marcus, 1985; Cattaneo-Viotti, 1986). I now readily recant from the position taken in an earlier publication (Willan, 1983) wherein I grouped the Umbraculidae and Tylodinidae together as a single family. My basis for doing so was Thiele's (1931) scheme of classification for the Opisthobranchia. Thiele followed Pilsbry (1896). Other authors who did not distinguish separate families in the suborder Umbraculacea have been Ghiselin (1965), Keen (1971), Thompson (1976) and Gosliner (1981).

Delineation of taxa at the family-level group within the



Pleurobranchacea (i.e. the "higher" Notaspidea of Minichev, 1970) is less straightforward. Following Odhner (1926), all genera of the Pleurobranchacea were placed in a single family, Pleurobranchidae, and this remains the most widely accepted classification (e.g. Pruvot-Fol, 1954; Er. Marcus, 1965; Thompson, 1970; Ev. Marcus and Er. Marcus, 1970; Willan, 1983, 1984b; Healy and Willan, 1984; Willan and Bertsch, 1987). But, following Burn (1962), a few authors treat the genera as comprising two (somewhat unfortunately named), separate families, Pleurobranchidae and Pleurobranchaeidae (Ev. Marcus, 1977; Ev. Marcus and Gosliner, 1984; Gosliner, 1985; Cattaneo-Vietti, 1986). Not one of these subsequent authors have discussed their basis for recognizing separate families or advanced further arguments to support it. Burn (1969) reverted seven years later to using one family, Pleurobranchidae, to encompass all pleurobranch genera and he continues to hold this view to the present time (R. Burn, pers. comm., 1986). I hope this paper sets forth sufficient reasons in support of the single family stance to convince other malacologists of its correctness.

The monophyletic origin of the Pleurobranchacea has never been challenged, based soundly as it is on many characters, apomorphies being: the internal, rectangular shell; presence of pedal gland; median buccal gland; internal, tubular vas deferens; protrusible penis. What is debated is the taxonomic category best suited to the two major pleurobranch subgroups. The characters splitting the Pleurobranchidae are: presence or absence of a shell; anal position; transverse width of oral veil, relationships of the mantle and head; location of rhinophores; papillae lining oral veil; mandibular element shape; presence or (secondary) absence of pedal gland. Only the third, fourth, fifth and sixth of these characters are apomorphies of the pleurobranchaeine branch (consisting of three genera) and none is an autapomorphy for the pleurobranchine branch (five genera). Outgroup comparison for the pleurobranchaeine branch reveals every one of the four apomorphies occurs (in whole or as apomorphic traits) in genera of the pleurobranchine branch [i.e. (i) shell-less *Berthellina* and *Pleurobranchus* species, (ii) forward anal position in *Berthella*, (iii) elongate-polygonal mandibular elements in *Bathyberthella*, and (iv) absence of a pedal gland in *Berthellina* and *Bathyberthella*]. Therefore, the essential divisions between the two pleurobranch subgroups are reduced to four, of which the three most important are interdependent (i.e. one cannot occur without the simultaneous occurrence of the other two). In this clade, fusion of the mantle and head anteriorly necessitated separation of the rhinophores and, as a consequence, the oral veil spread transversely. This being the case I find no grounds for recognition of separate families. I have already shown the division could not be justified on the characters Burn (1962) originally chose (Willan, 1983). Two of the characters employed by Burn in his definition of the separate families were: (i) gill rachis - smooth or transversely grooved (Pleurobranchidae), or tuberculate (Pleurobranchaeidae); (ii) mantle - generally larger than the foot (Pleurobranchidae), or generally smaller than the foot (Pleurobranchaeidae). Both are simply incorrect. To counteract the first point is the fact that all members

of the genus *Pleurobranchus* have a strongly tuberculate gill rachis. To counteract the second point are the facts that, in life, species of *Pleurobranchella* have a mantle that is larger than the foot (Ev. Marcus and Gosliner, 1984), and this is also true for *Pleurobranchaea obesa* (Gosliner, 1985); also *Bathyberthella antarctica* has a foot that is much larger than its mantle (Willan and Bertsch, 1987). Neither character, therefore, can be used to separate clusters of genera at any higher level whatsoever. Erzincioğlu and Unwin (1986) oppose, on philosophical grounds, the elevation of subfamilies to families.

In a later paper, Odhner (1939) recognized two subgroups within the Pleurobranchidae (as recognized by him). One (the berthelline group) being (to use the original definitive characters) small-sized with simple, non-tuberculate gill rachis, and the other (the pleurobranchine group) being large-sized with a tuberculate gill rachis. According to current concepts of generic boundaries, the genera *Berthella*, *Berthellina*, *Bathyberthella* and *Pleurehdera* would constitute the former group and *Pleurobranchus* would constitute the latter one by itself. Such a division based on relative size in conjunction with mantle and gill rachis texture cut right across the earlier scheme of Vayssière (1897, 1898) which united *Berthella* and *Pleurobranchus* and excluded *Berthellina*. This was because it was essentially based on radular characteristics. One of the principal objectives of my phylogenetic studies has been to evaluate these conflicting classifications.

To date, my investigations (on phylogenetics, phenetics, sperm ultrastructure and diets) all vindicate Odhner's (1939) scheme and they confirm the berthelline and pleurobranchine groups are natural, holophyletic clusters of genera. To complement the characters (of relative size, and mantle and gill rachis surface texture) originally used by Odhner, I have identified several additional significant ones. The group of berthelline genera has synapomorphies of triaulluc reproductive condition and penial gland. The other lineage (*Pleurobranchus*) has autapomorphies of deep anterior mantle cleft, rhinophoral pulsating activity in life, permanently exposed flaps surrounding the genital apertures of sexually mature animals, and tuberculate mantle and gill rachis. The acrosome of *Pleurobranchus* sperm is clearly periodically banded, the nucleus is relatively short, up to five nuclear keels are present and the glycogen piece is relatively short. In all the berthelline genera, the acrosome is not periodically banded (or very weakly so), the sperm nucleus is relatively long, there is a single nuclear keel or none at all and the glycogen piece is relatively long (Healy and Willan, 1984). All *Pleurobranchus* species presently known specialize on ascidians whereas the berthelline genera eat sponges [although one species, *Berthellina citrina*, is also able to eat scleractinian corals and sea anemones (Willan, 1984a)]. Burn (1962) formalized Odhner's system by naming these two lineages as new subfamilies, Berthellinae Burn and Pleurobranchinae Férussac. The characters discussed above, whilst confirming the existence of separate lineages, should not, I suggest, be used to justify subdivision at the subfamily level. That rank is too high and I recommend a ranking of tribe is more appropriate; thus the two tribes should be called Berth-

ellini Burn and Pleurobranchini Férussac.

One final point strengthening my argument for not elevating the taxonomic status of the berthelline and pleurobranchine groups to the level of subfamilies concerns relative body size. Burn (1962) used this character in his classification. Because it is a more subjective character than others, it should be considered apart from them. Relative size is probably valid to use to separate adults of most species of the Pleurobranchinae (i.e. *Pleurobranchus* species tend to attain 70 to 300 mm and are therefore "large" compared to members of the other genera that are "small" with sizes of 20 to 70 mm). It must, however, be remembered that we are dealing with highly deformable invertebrates that have indeterminate growth. For this reason, size cannot be used as a strict (and certainly not exclusive) taxonomic character. Several exceptions are already known that lessen its usefulness. For example, there are "small" species of *Pleurobranchus* (less than 70 mm crawling length - *P. ovalis*) and a species of *Bathyberthella* grows to over 120 mm in Antarctic waters (Willan and Bertsch, 1987).

Before leaving this section on families, I must highlight one alteration it has been necessary to incorporate into the taxonomic hierarchy given in Table 1. Authorship of the family Pleurobranchidae is usually credited to Menke, 1828, but it was actually introduced by Férussac (as "Les Pleurobranches") six years earlier (Férussac, 1822, pp. 26 and 29). Therefore, according to the principle of co-ordination embodied in the International Code of Zoological Nomenclature (I.C.Z.N., 1985, Article 36), authorship of the subfamily Pleurobranchinae and tribe Pleurobranchini must also be attributed to "Férussac, 1822".

## REAPPRAISAL OF GENERA

This is the section where I break ranks with strict cladists and employ judicious weighting of characters to obtain the "most correct" relationships between genera. All the eleven genera given in Table 1 are considered separately in this appraisal. The characters defining each are briefly enumerated and examined so as to consider relationships to other genera. Where necessary, the consideration ranges to reappraisals of synonymous taxa. In light of what has already been written in this paper, I feel that complete diagnoses, or even listing sets of apomorphies, for every genus would be profligate. The only exception is *Anidolyta* where a formal diagnosis has to be provided because a new taxon is being proposed. The sequence of presentation is phylogenetically systematic, starting with the most primitive genus and progressing to the most advanced.

### *Tylodina* Rafinesque, 1819

Type species, by subsequent designation (Pilsbry, 1896, p. 185), *Tylodina citrina* Joannis, 1834 (= *Patella perversa* Gmelin, 1790). Recent, Mediterranean Sea. Fig. 1.

Synonyms: *Parmophorus* Cantraine, 1835; *Joannisia* Monterosato, 1884; *Tylodinella* Mazzarelli, 1898.

This genus is unquestionably the most primitive in the order Notaspidea and among the most primitive of the en-

tire Opisthobranchia. This view is primarily based on the structure of the nervous and reproductive systems. The central nervous system consists of a ring of five discrete ganglia, two cerebral, two pleural and the visceral ganglion, the latter retaining its integrity (Vayssière, 1883; MacFarland, 1966; Gosliner, 1981). The reproductive system is monaulic with an external sperm groove leading from the genital aperture at the base of the right oral tentacle to the non-protrusible penis. Another very primitive feature is the osphradium. This organ (merely a small patch of sensory epithelium, lying close in front of, and slightly below, the anterior end of the gill rachis) was first described histologically by MacFarland (1966). The osphradium is innervated by a separate ganglion located immediately beneath it (Pelseneer, 1894; MacFarland, 1966). *Tylodina* possesses many other plesiomorphies for the order, the more significant of which are: the external shell; velar connection (albeit small) between the laterally slit oral tentacles; separate, dorso-ventrally slit rhinophores; smooth upper foot surface; presence of a pedal gland; gill location; smooth gill rachis; absence of a median buccal gland; two allosperm receptacles. *Tylodina* does possess some apomorphies however, these are to do with shell musculature, cuticularized labial ring, cuticularized papillae in anterior section of stomach and penial position. The last three of the characters just mentioned are, in fact, synapomorphies for *Tylodina* and its sister genus *Anidolyta*. The single apomorphy I can find for *Tylodina* is the interpolation of a special intermediate suspensor muscle in the gap between the ends of the crescentic columellar muscle.

Biogeographically, *Tylodina* is an enigmatic genus. Five species occupy restricted ranges in temperate waters, *T. perversa* in the eastern Atlantic and Mediterranean, *T. americana* in the western Atlantic, *T. fungina* in the eastern Pacific, *T. corticalis* in southern Australia, *T. alfredensis* in southern Africa. Only minor differences separate these species and, in fact, the characters separating them at the specific level are uncertain. Whilst I think Thompson (1970) was incorrect in suggesting all these species be merged into one, I do accept the opinion of Pruvot-Fol and Fischer-Piette (1934) that all the nominal taxa based on Mediterranean specimens are synonymous.

### *Anidolyta* gen. nov.

Type species, here designated, *Tylodina duebeni* Lovén, 1846. Recent, North Atlantic Ocean.

Synonyms: *Tylodina* Lovén, 1846 (non Rafinesque, 1819); *Roya* Bertsch, 1980 (non Iredale, 1912).

Diagnosis: Small notaspideans bearing an external, oval, patelliform shell (approximately 10 mm in length). Mantle margin crenulate or minutely papillate. Columellar muscle crescentic; incomplete on right side; gap not filled by intermediate suspensor. Oral tentacles slit laterally; joined to each other by a small veil (buccal shield). Rhinophores slit dorso-ventrally; without any proximal connection. Gill a short plume on right side; attached to body for half its length. Genital apertures at base of right oral tentacle. Radula broad, ptenoglossan; rows lacking a rachidian; laterals very

numerous, bearing 2 or 3 strong denticles on blade below cusp, not showing differentiation across rows.

*Anidolyta* remains the most enigmatic genus of the order. In the first place this is due to the scarcity of specimens, less than five being known. Actually all published descriptions rely on only three, i.e. the holotype of *Tyrodina duebeni* (Odhner, 1939) and two *Roya spongotheras* (Bertsch, 1980). In addition to this difficulty, is the problem of the genus' confused taxonomic history. Odhner (1939) placed Lovén's *Tyrodina duebeni* in the genus *Tyrodinella* Mazzarelli on account of Mazzarelli's (1898) published description. I am certain Mazzarelli's account of his *Tyrodinella tranchesii* relates to a juvenile *Tyrodina perversa*. The similarities are overwhelming: pale yellow animal; thin, circular, conical shell; small oral veil; eyes; position of gill, anus and penis; structure of gill, radula and central nervous system; division of stomach into anterior cuticularized and posterior thin-walled regions. The fact that the animal of *Tyrodinella tranchesii* could be completely accommodated within its shell merely indicates it was a juvenile specimen and its immaturity must have resulted in Mazzarelli's misunderstanding of the reproductive system. Mazzarelli (1898) apparently never saw a specimen of *T. perversa*. The only irreconcilable difference between Mazzarelli's specimen and *T. perversa* is the absence of a rachidian row in the former. Ev. Marcus (1985) supposed, probably perfectly correctly, that these very fine teeth had been lost during Mazzarelli's preparation of the radula. When in 1979, Dr. H. Bertsch received another species that was obviously congeneric with *T. duebeni*, he consulted Mr. R. Burn and myself over the matter. It was obvious that a new genus was needed. I suggested *Roya* might be suitable by virtue of its conchological, periostracal and radular similarities. However this suggestion was not correct because Marshall (1981) subsequently showed *Roya* to be a basomatophoran pulmonate related to *Siphonaria*. Marshall considered *Roya* as a junior synonym of *Williamia*. Rehder (1984) reiterated Marshall's information. In passing, I must add that Marshall (1981, p.488) erred in stating *R. spongotheras* had a rachidian tooth; he was actually referring to an illustration of *Tyrodina fungina*. Since neither *Tyrodinella* nor *Roya* can fill the void as a genus for *T. duebeni* and *R. spongotheras*, I provide the new name *Anidolyta* (an anagram of the word tyrodina with feminine termination) for them both with Lovén's species selected as type. Ev. Marcus, to whom I conveyed all the above information during correspondence in 1983, has unintentionally already published the name *Anidolyta* (Ev. Marcus, 1985), but her usage represents a *nomen nudum* being devoid of diagnosis or indication of type species. It was unfortunate her paper appeared before this one of mine.

*Anidolyta* is the hardest genus in the whole order to delineate fully or separate adequately from other umbraculacean genera because of the lack of comparative anatomical data. Without question it is closest to *Tyrodina*, the two being sister groups. *Anidolyta* and *Tyrodina* share numerous synapomorphies (already given here under *Tyrodina*). Differences between them relate to shell musculature (an intermediate suspensor is present in *Tyrodina*), mantle margin (that of *Anidolyta* is crenulate or papillate), rachidian tooth

(absent in *Anidolyta*) and denticles on lateral teeth (present in *Anidolyta*). Actually, only the final character can be construed as an autapomorphy for *Anidolyta* with any certainty.

As it is presently conceived, *Anidolyta* is a small genus consisting of two [and possibly a third (Marshall, 1981)] species. They are distinguished primarily by their shells and radular proportions. The shell of *A. duebeni* is conical and parallel-sided, and the protoconch is located behind the centre; that of *A. spongotheras* is circular, extremely flattened, and the protoconch is central. There are relatively more teeth in the radula of *A. spongotheras*. Most specimens of these two species have been trawled below 350 m.

#### *Umbraculum* Schumacher, 1817

Type species, by monotypy, *Patella umbraculum* Lightfoot, 1786. Recent, cosmopolitan in tropical and warm temperate seas. Fig. 2.

Synonyms: *Patella* Lightfoot, 1786 (non Linnaeus, 1758); *Acado* Lamarck, 1801 (non Commercon, 1792); *Gastroplox* Blainville, 1819; *Umbrella* Lamarck, 1819; *Ombrella* Blainville, 1824; *?Spiricella* Rang, 1827; *Umbrella* Orbigny, 1841; *Operculatum* H. Adams and A. Adams, 1841.

*Umbraculum* is a unique opisthobranch genus; one that possesses more specialized, derived characters than any other notaspidean. This implies a long separation for *Umbraculum* from the tyrodinids, with which it shares an external, patelliform shell and cuticularized labial ring, and even longer separation from the pleurobranchs. *Umbraculum* has undergone considerable reorganization of the body and mantle/gill complex and it has also acquired many autapomorphies, the most significant of which are: flattened shell; voluminous and tough, pustulose foot with deep anterior cleft containing the mouth and non-protrusible penis; two pairs of oral tentacles; lengthening of the gill; broadening of the radula; location of anus posterior to gill basement membrane. No doubt, as more examinations of *Umbraculum* are conducted, more apomorphies will be revealed, e.g. the enormous lengthening of the spermatozoon (Thompson, 1973). The sperm nucleus, which is also very long, is coiled around the axoneme and anterior portion of the mitochondrial derivative. In addition, the centriolar derivative and anterior extension of the mitochondrial derivative are located very close to the axoneme (Healy and Willan, 1984).

Moquin-Tandon's (1870) monograph still stands as the foremost reference source for comparative anatomical detail of *Umbraculum*. Some of the inaccuracies of Moquin-Tandon's description of the reproductive system were corrected by O'Donoghue (1929), Ev. Marcus and Er. Marcus (1967), and Ev. Marcus (1985), but physiological and histological studies are still urgently required to understand the functioning of its complicated reproductive system.

The genus *Umbraculum* is either monotypic as Burn (1959) has suggested (in which case the species should take the earliest available name *Umbraculum umbraculum* Lightfoot, 1786), or bitypic (Thompson, 1970). The literature, right up to the present day, contains a plethora of names most of which are certainly synonyms of *U. umbraculum*.

*Pleurobranchus* Cuvier, 1804

Type species, by monotypy, *Pleurobranchus peronii* Cuvier, 1804. [Thompson's (1970, p. 179) designation of *Bulla membranacea* Montagu, 1815 as type species is invalid.] Recent, Indo-Pacific Ocean. Fig. 3.

Synonyms: *Oscanius* Gray, 1847; *Susania* Gray, 1857; *Oscaniella* Bergh, 1897.

Pleurobranchs belonging to this long-established genus are relatively large-sized as adults (e.g. *Pleurobranchus grandis* can attain 210 mm) and have apomorphies of tuberculate mantle and gill rachis, cleft anterior mantle border and, in mature adults, flaps surrounding the genital apertures. In addition, the tips of the rhinophores regularly pulsate in living specimens. The large body size, absence of a penial gland and generally simple radular tooth shape point to *Pleurobranchus* as being the least modified genus of the Pleurobranchinae. *Pleurobranchus* is probably nearer to the common ancestor than any genus of the berthelline tribe and hence it shares some characters with *Pleurobranchella*, the genus occupying the same relative position in the Pleurobranchaeinae.

In view of this long history, it is not surprising to note that *Pleurobranchus* possesses a relatively large number of characters showing apomorphic traits (i.e. shell sometimes absent, shell size, shell location, mantle to shell ratio, single denticle at base of some radular teeth, one or two allosperm receptacles, prostate gland condition). Because it seems to be a large genus numerically, authors have attempted to split *Pleurobranchus* (presumably on the assumption that it was paraphyletic) by creating or recognizing genera based on one or a few of these apomorphic traits. Such attempts have been unsuccessful because these traits do not occur concordantly, and I agree with Thompson (1970) and Baba and Hamatani (1971) in recognizing only *Pleurobranchus*. *Oscanius* is the first of three such sometime recognized genera; its characters being the shallow anterior mantle notch, single denticle on blade of mandibular element, large and thin (uncalcified) shell, innermost lateral radular teeth with a basal denticle (Burn, 1962). However outgroup comparison (with the Berthellini) shows several species there that possess identical character states. Neither has *Oscanius* a single apomorphy; so it cannot be separated, even as a subgenus, from *Pleurobranchus*. *Susania* in another such genus; its characters being the thick mantle, deep anterior mantle notch, several denticles on blade of mandibular element, shell absent or present (in which case it is very small, oval, calcareous and located posteriorly) (Burn, 1962). The only apomorphies possessed by *Susania* are the greatly thickened mantle and small shell. *Oscaniella* is the third such genus; its characters being the relatively small mantle tubercles, small, anteriorly-located shell and lack of flaps surrounding the genital aperture (Bergh, 1897, 1905). The final character is erroneous - probably Bergh's animals were immature. The other two characters are either possessed by other species of *Pleurobranchus* or are homeoplasies of other pleurobranchine species. Recognition of *Oscanius*, *Susania* or *Oscaniella* as genera or subgenera, based solely on one character (out of all of these given above), is completely unjustified.

In an earlier paper (Willan, 1983), I was equivocal about the status of *Pleurobranchus* and its relationship to *Berthella*, reflecting the uncertainty in the existing literature. It is now clear that both *Pleurobranchus* and *Berthella* are distinct genera and not particularly closely related, their shared character states being symplesiomorphies or homeoplasies.

*Pleurobranchus* species have wide distribution ranges in tropical waters of the Mediterranean, Indian, Pacific and Atlantic Oceans. The apparent absence or rarity of *Pleurobranchus* species from the coral atolls of the central Pacific region (Willan, 1984b) is inexplicable at present. Diversity of *Pleurobranchus* species decreases rapidly in temperate waters where, in general, they are replaced (phylogenetically not ecologically) by *Berthella* species.

*Berthella* Blainville, 1825

Type species, by original designation, *Berthella porosa* Blainville, 1825 (= *Bulla plumula* Montagu, 1803). Recent, North Atlantic Ocean. Fig. 4.

Synonyms: *Cleanthus* Gray, 1847; *Bouvieria* Vayssièrè, 1896; *Gymnotoplax* Pilsbry, 1896; *Berthellinops* Burn, 1962.

The genus *Berthella* has unfortunately had a tortuous taxonomic history because it was confused with *Berthellina* (Gardiner, 1936; Odhner, 1939). Its generic nomenclature is now settled. Willan (1978) examined the holotype of *Gymnotoplax americanus* Verrill and showed that it was a species of *Berthella* with the mantle mutilated to such a degree the shell had become uncovered.

It is probable that *Berthella* formed the stock from which other Recent genera of the tribe in Berthellini evolved—*Bathyberthella*, *Pleurehdera* and *Berthellina*. In *Berthella* there is a pool of characters showing apomorphic traits. Several of these traits also occur in other pleurobranchine genera, for example the relatively large shell (covering the whole of the viscera), a denticle at the base of some of the lateral teeth, smooth blades to the mandibular elements, reduction of the number of allosperm receptacles to one and a distinct prostate gland. Others are unique to *Berthella* i.e. mantle autotomy and anal site in front of the middle of the gill's suspensory membrane. Like *Pleurobranchus*, *Berthella* appears to have had a long evolutionary history, but unlike *Pleurobranchus*, malacologists have not attempted to split *Berthella* into other genera. When the anatomy of more species is known, a division into subgenera may be possible. Characters that should repay further attention in this context are the mantle (i.e. spicules, fine structure of epithelial and sub-epithelial glands), anal position, reproductive system, autotomy and feeding behavior.

*Berthella* is a moderately large genus with its constituent species widespread geographically and bathymetrically. Several species are common in the intertidal and shallow subtidal zones where they play a significant role in structuring encrusting communities by grazing sponges (Cattaneo, 1982; Willan, 1984a; Willan and Morton, 1984).

*Bathyberthella* Willan, 1983

Type species, by original designation, *Bathyberthella*

*zelandiae* Willan, 1983. Recent, New Zealand.

*Bathyberthella* is the most recently characterized pleurobranch genus. Rather than being erected to contain a number of existing species, *Bathyberthella* was created to accommodate initially one (now two) newly described species from deep water. Its external features resemble those of *Berthella*, *Berthellina* and *Pleurehdera* and many of its characters, both external and internal, are symplesiomorphies shared with those three genera, i.e. smooth non-emarginate mantle, smooth gill rachis, simple radular teeth, prostatic dilation of vas deferens, triaulic reproductive system. However, *Bathyberthella* does possess four important, internal apomorphies: a very large, flexible, cuticular shell; long; tubular median buccal gland (that is apparently not branched distally); narrow, erect radular teeth; narrow, oval or elliptical mandibular elements that lack lateral processes and have an irregularly denticulate anterior margin. One species of *Pleurobranchus*, *P. membranaceus*, also possesses an uncalcified cuticular shell. That homeoplasious state must have, therefore, occurred congruently in the two genera; occurring as an apomorphy in *Bathyberthella* and an apomorphic trait in *Pleurobranchus*. In the phylogenetic analysis (Fig. 20), no apomorphy could be found to link *Bathyberthella* more closely to either the *Berthella* branch or the *Berthellina/Pleurehdera* branch. In the strictly dichotomous dendrogram (Fig. 21), *Bathyberthella* was located as a sister group to *Berthella*.

The "unexpected amalgam of characters" (Willan, 1983) possessed by *Bathyberthella* are the reasons for the slight differences in its placing between the cladogram and dendrogram. Indeed, *Bathyberthella* is a most significant genus. The form of its mandibular elements is highly important and difficult to explain. Its mandibular elements are narrow and oval (i.e. of the polygonal type) with denticulate anterior margins. Previously, I had interpreted the form of these elements as indicative of a relationship with the Pleurobranchaeinae (Willan, 1983), but it is now apparent that the affinities of *Bathyberthella* lie wholly with the genera of the Pleurobranchinae, and in particular, the tribe Berthellini (Willan and Bertsch, 1987). One symplesiomorphy of this subfamily is possession of mandibular elements of the cruciform type (present in every species of all the other four genera), so the occurrence of the polygonal ones mentioned above in *Bathyberthella* is most unexpected. There are two opposing hypotheses to account for the presence of polygonal elements. Either *Bathyberthella* represents the termination of a lineage that stemmed independently from the very base of the Pleurobranchinae (i.e. its mandibular elements retain the plesiomorphic, ancestral state) or it has lost the cruciform elements of others of its tribe and acquired new ones anatomically convergent with those of the ancestor. I favoured the former hypothesis because it was more parsimonious when describing *Bathyberthella*, but have subsequently rejected it because all the other characters tie *Bathyberthella* so firmly with the rest of the tribe Berthellini.

The two species of *Bathyberthella* are allopatric. Each apparently occupies a restricted geographic range and each possesses apomorphies of its own. *B. zelandiae* occurs below 1600 m on the Bounty Trough, southwest of New Zealand.

It has an enlarged buccal mass that can be protruded for up to half the body length, large eyes (unusual for an abyssal mollusc), 4-14 denticles (mean = 10.14) on the anterior border of the mandibular elements, and minute papillae on the rhinophores and oral veil (Willan, 1983). *B. antarctica* is known from 128 to 486 m in waters bordering the Antarctic continent. It's apomorphies are large size (specimens are approximately 120 mm long when adult, making it easily the largest member of the Berthellini); disproportionate enlargement of the foot with respect to the mantle; subterminal site of the protoconch with respect to the teleconch; very long median buccal gland, 1 to 5 denticles (mean 3.25) on the anterior border of the narrow mandibular elements; enlargement of the ovotestis; loss of penial gland (Willan and Bertsch, 1987). Probably these apomorphies represent adaptations by *B. antarctica* to the Antarctic environment.

*Pleurehdera* Er. Marcus and Ev. Marcus, 1970

Type species, by original designation, *Pleurehdera haraldi* Er. Marcus and Ev. Marcus, 1970. Recent, Tuamotu Archipelago, Pacific Ocean. Fig. 5.

*Pleurehdera* is the most weakly characterized of any of the tribe Berthellini and it is very close to *Berthellina*. Its sole character that could be held up as an apomorphy is the greatly enlarged pedal gland that is supposed to take up almost half the foot sole and occupy the full width of this posterior section (Er. Marcus and Ev. Marcus, 1970). It is important however to note that a later investigation of new material failed to reveal any such gland (Willan, 1984b), so its presence in the unique holotype might have been an artifact of preservation. Even so, *Pleurehdera* shows no relationships with *Pleurobranchus* as claimed by Er. Marcus and Ev. Marcus (1970) on the pedal gland alone, since this gland is now known to be present in sexually mature individuals of many species of the subfamily Pleurobranchinae. Characters separating *Pleurehdera* from *Berthellina* are the relatively larger shell and low point of origin of the receptaculum seminis off the vagina in *Pleurehdera* (both character states occur elsewhere in the Berthellini), and form of the radula. In *Pleurehdera*, the teeth are elongate, the innermost laterals possess a single denticle at their base and middle laterals possess a denticle near the cusp (Er. Marcus and Ev. Marcus, 1970; Willan, 1984b).

*Pleurehdera* is a monotypic genus. *P. haraldi* probably occurs throughout the tropical, central Pacific Ocean. Its known depth range is from 3 to 12 m. Willan (1984b) has redescribed *P. haraldi* on the basis of material from the Marshall Islands.

*Berthellina* Gardiner, 1936

Type species, by original designation, *Berthellina engeli* Gardiner, 1936. Recent, North Atlantic Ocean. Fig. 6. Synonym: *Berthella* Vayssière, 1896 (non Blainville, 1825).

The distinctive lamellate shape of the radular teeth (very elongate with numerous denticles on the posterior face of the distal half of the blade) is the major autapomorphy possessed by species of this genus. The pedal gland has been lost. Apomorphic traits are for a small and spatulate shell

(or none at all), for the shell to be located centrally or anteriorly above the viscera, for the anterior mantle margin to be entire or weakly emarginate, and for the blades of the mandibular elements to be smooth or very weakly denticulate. In attaining only small adult size and possessing a smooth mantle and gill rachis, species of *Berthellina* are indistinguishable in body form externally from species of the other three genera of the tribe Berthellini.

*Berthellina* is not a speciose genus, there being fewer than six valid species. However the genus is well known because some of its constituent species are widespread geographically (e.g. *Berthellina citrina*) and rather common. All species occur in tropical and warm temperate waters and they range from the intertidal zone to moderate subtidal depths.

*Pleurobranchella* Thiele, 1925

Type species, by monotypy, *Pleurobranchella nicobarica* Thiele, 1925. Recent, Indian Ocean.

Synonyms: *Pleurobranchoides* O'Donoghue, 1929; *Gigantotum* Guangyu and Si, 1965.

Anatomical data are gradually being accumulated on this interesting genus. Such data have been unavailable in the past because of paucity of material. O'Donoghue's (1929) account of *Pleurobranchoides gilchristi* is the most complete of any of the descriptions of new species. Er. Marcus and Ev. Marcus (1970) first mentioned the similarity of *Pleurobranchoides* to *Pleurobranchella*. Willan (1977) synonymized both genera as well as *Gigantotum*. Ev. Marcus and Gosliner (1984) regarded *Pleurobranchella* as monotypic but preferred to consider *Gigantotum* as "a distinct but doubtful genus" on the ground that its reproductive system had not been described.

Willan (1977) has already presented a definition of *Pleurobranchella*. It is important, at this time, to separate the plesiomorphies from the apomorphies contained in that definition. Several of the characters of *Pleurobranchella* represent plesiomorphies for the subfamily Pleurobranchaeinae (and in fact the family Pleurobranchidae too); these are: the very large mantle that covers the foot laterally and posteriorly; simple radular teeth; polygonal mandibular elements with denticulate anterior edges; dialuc reproductive condition; two allosperm receptacles. Most of these characters are also plesiomorphies for the *Pleurobranchella* - *Pleurobranchaea* lineage. On the other hand *Pleurobranchella* does possess three apomorphies for the *Pleurobranchella*-*Pleurobranchaea* lineage: tuberculate mantle; broadly expanded oral veil; muscle penial sac accommodating coils of the distal vas deferens. Finally *Pleurobranchella* possesses four apomorphies of its own: loss of pedal gland; tuberculate gill rachis; distinct prostate gland; penial papillae. However, the latter three specializations are apparently only possessed by some species (i.e. they are apomorphic traits). Outgroup comparison reveals not one of these four apomorphies to be unique to *Pleurobranchella*: the pedal gland has also been lost independently in *Berthellina*; *Pleurobranchus* also has a tuberculate gill rachis; *Umbraculum* also has a distinct prostate gland; *Euselenops* has penial papillae. Because *Pleuro-*

*branchella* retains so many primitive characters and so few unique derived ones, Willan (1977) hypothesized that it was closer to the ancestor of the pleurobranchaeine stem than either *Pleurobranchaea* (its sister group) or *Euselenops*. Nothing revealed in this study has altered that opinion. Thus *Pleurobranchella* is specially significant because it is the most primitive extant genus in the most advanced pleurobranch subfamily. There is every reason to believe *Pleurobranchella* represents a relict genus.

There are probably less than four biological species of *Pleurobranchella* worldwide. Indeed, as Ev. Marcus and Gosliner (1984) indicated, the genus may be monotypic. The genus is widespread in the tropical Indian and western Pacific Oceans. All material has come from depths greater than 200 m. Natural diet is unknown, but there is one record of predation on juvenile *Pleurobranchaea* (Eales, 1937).

*Pleurobranchaea* Meckel in Leue, 1813

Type species, by subsequent monotypy (Blainville, 1825, p. 376), *Pleurobranchidium meckelii* Blainville, 1825. Recent, Mediterranean Sea. Fig. 7.

Synonyms: *Pleurobranchidium* Blainville, 1825; *Cyanogaster* Blainville 1825; *Koonsia* Verrill, 1882; *Pleurobranchillus* Bergh, 1892; *Macfarlandaea* Ev. Marcus and Gosliner, 1984 (syn. nov.).

*Pleurobranchaea* and *Pleurobranchella* represent sister groups with *Pleurobranchaea* the more speciose and variable. Unfortunately many of its nominal species are insufficiently described (Er. Marcus and Ev. Marcus, 1966; Willan and Bertsch, 1987), and this lack of comparative data hampered my tabulation of character states for this genus. Now that species of *Pleurobranchaea* are regularly used in neurophysiological research (e.g. Davis, 1975; Siegler, 1977a, b; McClelland, 1983), nontaxonomists should be aware that much of the literature on *Pleurobranchaea* is burdened under a plethora of unrecognizable synonyms. Future descriptions of novel species and appraisals of existing ones must take ontogenetic and intraspecific variation into account. No additional species should be based on a holotype that is immature.

Gosliner (1985) has recently reiterated the proposition that *Koonsia* is a junior synonym of *Pleurobranchaea* (Willan, 1977, 1983). Besides being taxonomically unnecessary, the recently described taxon *Macfarlandaea* is unsound because both (the only two) characters used to define it (Ev. Marcus and Gosliner, 1984, p. 40) are wrong (i.e. not possessed by the type species). Contrary to Ev. Marcus and Gosliner's definition that *Macfarlandaea* has "rudimentary secondary cusps on all radular teeth", MacFarland (1966, p. 90, pl. 15, figs. 16, 17, 21) clearly indicated their absence, in *P. californica*, from the first row of laterals as well as from several of the outermost rows of lateral teeth. The statement "Pleurembolic penis with cuticular stylet" is also invalidated by MacFarland's account of *P. californica* (MacFarland, 1966, p. 99, pl. 17, figs. 1, 2); the penis of that species is actually muscular and filiform, and there is no stylet whatsoever.

Two characters appear for the first time (as apomorphic traits) in *Pleurobranchaea*, posterior fusion of the mantle and foot, and a caudal spur on the upper surface of

the tail. The median buccal gland is enlarged in *Pleurobranchaea* so that its network of tubules extends between all the organs at the front of the visceral cavity (Willan, 1975; Morse, 1984). All species of *Pleurobranchaea* have reduced the size of the mantle. Other apomorphies are difficult to find; I think this is not because they do not exist (*Pleurobranchaea* is undoubtedly holophyletic), but because they have not been looked for. For example, initial investigations into the ultra-structure of its sperm revealed a very short glycogen piece that was devoid of any axonemal remnant (Healy and Willan, 1984).

Species of *Pleurobranchaea* occur in temperate waters in both hemispheres. In view of this wide distribution and relative abundance of certain species, it is surprising that so little is known conclusively of the natural diet. The only generalizations that can be made are that *Pleurobranchaea* species are active, opportunistic carnivores eating whole soft-bodied invertebrates or scavengers, and that cnidarians are amongst the more preferred food items (Willan, 1984a).

#### *Euselenops* Pilsbry, 1896

Type species, by monotypy, *Pleurobranchus luniceps* Cuvier, 1817. Recent, Indo-Pacific Ocean. Fig. 8.

Synonyms: *Neda* H. Adams and A. Adams, 1854 (non Mulsant, 1851); *Oscaniopsis* Bergh, 1897.

The genus is monotypic with its sole species, *Euselenops luniceps*, being widely distributed throughout the Indo-Pacific Ocean. Because of this extensive range and accessibility (*E. luniceps* occurs relatively abundantly in moderately shallow water), sufficient specimens have been collected to allow its anatomy to be described thoroughly (e.g. Bergh, 1897; Vayssière, 1901; O'Donoghue, 1929; Guangyu and Si, 1965; Thompson, 1970). In addition, its intraspecific variability is now understood and this has proved not to be great.

The external features of *Euselenops luniceps* are so distinctive that it was segregated into a subgenus distinct from *Pleurobranchaea* in the first synthesis of the Notaspidea (Pilsbry, 1896); this was even before its internal anatomy was known. Detailed anatomical studies laid even greater emphasis on its external diagnostic characteristics (Bergh, 1897; Vayssière, 1901), and *E. luniceps* was soon placed in a genus of its own. No malacologist has challenged this generic placement subsequently. Actually, the most notable apomorphies of *Euselenops* are external, i.e. the reduction of the mantle, the permanent mid-posterior mantle crenulation, the enlargement and increased flexibility of the foot, the enormous enlargement of the oral veil. All these apomorphies are probably related to the newly assumed habit of shallow burrowing, a behavior never displayed by other pleurobranchaeines. The mantle's smoothness is, by contrast, a plesiomorphy for this subfamily. The internal systems of *Euselenops*, particularly the alimentary and reproductive systems, are relatively conservative with the majority of characters showing the plesiomorphic state for the subfamily, e.g. the relatively small median buccal gland, simple radular teeth, absence of coiling of vas deferens within a penial sac. However, the presence of many papillae on the penis undoubtedly

represents one internal apomorphy. O'Donoghue (1929) described the nervous system as being distinct from all other genera in the Pleurobranchidae.

*Euselenops luniceps* appears to be the most advanced member of the Pleurobranchidae. It certainly represents the culmination of pleurobranch evolution as regards behavioral sophistication; it is highly active and carnivorous, and it can swim. Unfortunately we are completely ignorant of its diet (Willan, 1984a). Therefore studies on feeding and breeding behavior are urgently needed for *E. luniceps*.

## CONCLUSION

The purpose of this investigation has been a consideration of phylogenetic relationships within the notaspidean opisthobranchs. This study has, by application of Hennigian methodology, generated a phylogenetic hypothesis. Confirmation for this hypothesis came from computer analysis. Once anatomical data is available, it should be possible to explore relationships between the Notaspidea and other groups of opisthobranch gastropods more thoroughly. Again, the Hennigian approach should prove enlightening.

The hypothesis presented in this paper advocates a monophyletic origin for the Notaspidea. Significant characters uniting all members are the longitudinally-slit rhinophores (obviously derived from the cephalaspidean head shield); broad velar connection between the oral tentacles, lateral bipinnate gill, and anal site at the rear of the gill. A fundamental division soon split the notaspidean stock and the resulting divergent evolution, with concomitant trends of shell reduction and re-establishment of bilateral symmetry, produced the umbraculaceans and the pleurobranchaceans. The umbraculaceans dichotomized again to result in the conservative Tyloidiidae and the peculiarly specialized Umbraculidae whilst the pleurobranchaceans maintained their homogeneity. The considerable set of pleurobranchacean apomorphies is proof of that group's monophyly. Major pleurobranchacean evolutionary trends are for shell reduction, fusion of mantle with head (anteriorly) and tail (posteriorly), and dietary radiation. Although there are good reasons to support Minichev's (1970) contention that the Nudibranchia is paraphyletic, there being two fundamentally different groups, the Anthobranchia (= Doridacea) and Cladobranchia (= Dendronotacea, Armirancea and Aeolidacea), I seriously doubt his arguments in favour of evolution of one or both these nudibranchiate groups from notaspideans. Some basic relationships do exist between notaspideans and anthobranchs, symplesiomorphies being details of gill innervation, joint existence of visceral "blood glands", similar circulatory systems, ptenoglossan radulae, two jaws, lack of branching of digestive gland, sponge diet and possession of two allosperm receptacles. Both groups probably evolved from the same cephalaspidean group simultaneously. However, because each group has subsequently acquired so many specialized derived characters I see no advantage in lumping them together into one order. The origins of the cladobranchs are still more vexing; they most certainly cannot be derived from "higher notaspideans" as Minichev suggested.

This study of the order Notaspidea has presented one hypothesis for its evolution. It now only remains to translate that hypothesis into a taxonomic (= Linnaean) hierarchy (Table 6). In fact, this hypothesis generally supports the classification that already exists (Table 1). The fundamental notaspidean divisions are best recognized as suborders. Within the Umbraculoidea is a sole superfamily, Tylodinoidea<sup>1</sup>, with two families, Tylodinidae (containing two genera) and Umbraculidae (containing only one genus). Within the Pleurobranchacea is one superfamily, Pleurobranchoidea, and family, Pleurobranchidae, with two subfamilies, Pleurobranchinae (containing five genera) and Pleurobranchaeinae (containing three genera). Two tribes, Pleurobranchini (containing only *Pleurobranchus*) and Berthellini (containing *Berthella*, *Bathyberthella*, *Pleurehdera* and *Berthellina*), warrant separate recognition within the subfamily Pleurobranchinae.

**Table 6.** Revised higher classification of the Notaspidea.

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Order Notaspidea Fischer, 1883
Suborder Umbraculoidea Dall, 1889
Superfamily Umbraculoidea Dall, 1889
Family Tylodinidae Gray, 1847
Genus <i>Tyloclina</i> Rafinesque, 1819
Genus <i>Anidolyta</i> Willan, nov.
Family Umbraculidae Dall, 1889
Genus <i>Umbraculum</i> Schumacher, 1817
Suborder Pleurobranchacea Férussac, 1822
Superfamily Pleurobranchoidea Férussac, 1822
Family Pleurobranchidae Férussac, 1822
Subfamily Pleurobranchinae Férussac, 1822
Tribe Pleurobranchini Férussac, 1822
Genus <i>Pleurobranchus</i> Cuvier, 1805
Tribe Berthellini Burn, 1962
Genus <i>Berthella</i> Blainville, 1825
Genus <i>Bathyberthella</i> Willan, 1983
Genus <i>Pleurehdera</i> Ev. Marcus and Er. Marcus, 1970
Genus <i>Berthellina</i> Gardiner, 1936
Subfamily Pleurobranchaeinae Pilsbry, 1896
Genus <i>Pleurobranchella</i> Thiele, 1925
Genus <i>Pleurobranchaea</i> Meckel in Leue, 1813
Genus <i>Euselenops</i> Pilsbry, 1896

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## LITERATURE CITED

- Baba, K. and I. Hamatani. 1971. Description of *Pleurobranchus semperi* (Vayssière, 1896) from Osaka Bay, Middle Japan (Gastropoda: Notaspidea). *Veliger* 13(4):326-329.
- Bergh, L. S. R. 1897. Die Pleurobranchiden. - *Pleurobranchaea*. In: *Reisen im Archipel der Philippinen von Dr. C. Semper, Malacologische Untersuchungen* 7(1), C. G. Semper, ed. pp. 1-51.
- Bergh, L. S. R. 1898. Die Pleurobranchiden. - *Pleurobranchus*. In: *Reisen im Archipel der Philippinen von Dr. C. Semper, Malacologische Untersuchungen* 7(3), C. G. Semper, ed. pp. 117-158.
- Bergh, L. S. R. 1902. Die Pleurobranchiden. - *Acteon* . . . *Oscaniella*. In: *Reisen im Archipel der Philippinen von Dr. C. Semper, Malacologische Untersuchungen* 7(7), C. G. Semper, ed. pp. 313-382.
- Bergh, L. S. R. 1905. Die Opisthobranchiata der Siboga Expedition. *Siboga Expedition Reports* 50:1-248.
- Bertozzi, A. 1983. Occurrence of *Umbraculum mediterraneum* (Lamarck, 1819) around the Tuscan Archip. *La Conchiglia* 172-173:8.
- Bertsch, H. 1976. Intraspecific and ontogenetic radular variation in opisthobranch systematics (Mollusca: Gastropoda). *Systematic Zoology* 25(2):117-122.
- Bertsch, H. 1980. A new species of Tylodinidae (Mollusca: Opisthobranchia) from the Northeastern Pacific. *Sarsia* 65:233-237.
- Brundin, L. 1968. Application of phylogenetic principles in systematics and evolutionary theory. In: *Nobel Symposium 4. Current Problems in Lower Vertebrate Phylogeny*. T. Orvig, ed. pp. 473-495. Alquist and Wiksell, Stockholm.
- Burn, R. 1959. Comments on the Australian umbraculocean Mollusca. *Journal of the Malacological Society of Australia* 1(3):28-30.
- Burn, R. 1960. On *Tyloclina corticalis* (Tate), a rare opisthobranch from South-Eastern Australia. *Journal of the Malacological Society of Australia* 1(4):64-69.
- Burn, R. 1962. On the new pleurobranch subfamily Berthellinae (Mollusca: Gastropoda); a revision and new classification of the species of New South Wales and Victoria. *Memoirs of the National Museum, Melbourne* 25:129-148.
- Burn, R. 1969. A memorial report on the Tom Crawford collection of Victorian Opisthobranchia. *Journal of the Malacological Society of Australia* 1(12):64-106.
- Cattaneo, R. 1982. Opisthobranch molluscs of the Sorrentine Peninsula caves. *Bolletino dei Musei di Istituto di Biologica, Università di Genova* 50 (Suppl):376-377.
- Cattaneo-Vietti, R. 1986. On Pleurobranchomorpha from Italian Seas (Mollusca: Opisthobranchia). *Veliger* 28(3):302-309.
- Cox, L. R. 1960. General characteristics of Gastropoda. In: *Treatise on Invertebrate Paleontology, Part I, Mollusca 1*. J. B. Knight,

<sup>1</sup>Terminations for superfamilies and tribes follow Recommendation 29A of the most recent edition of the International Code of Zoological Nomenclature (I.C.Z.N. 1985).



- et al., eds. pp. 184-169. Geological Society of America and University of Kansas, Boulder, Colorado and Lawrence, Kansas.
- Cuvier, G. L. C. F. D. 1812. *Recherches sur les Ossements Fossiles de Quadrupèdes, où l'on rétablit les caractères de plusieurs espèces d' Animaux que les révolutions du Globe paroissent avoir détruites, etc.* Deterville, Paris, 4 vols.
- Cuvier, G. L. C. F. C. 1817. *Le Règne Animal distribué de'après son organisation, pour servir de base à l'histoire naturelle des Animaux et d'introduction à l'Anatomie Comparée.* Paris. 4 vols.
- Davis, W. J. 1975. Organizational concepts in the central motor networks of invertebrates. *Advances in Marine Biology* 18:265-292.
- Eales, N. B. 1937. Apparent viviparity in *Pleurobranchoides*. *Proceedings of the Malacological Society of London* 22(6):371-374.
- Eales, N. B. 1938. A systematic and anatomical account of the Opisthobranchia. John Murray Expedition 1933-34. *Scientific Reports of the British Museum (Natural History)* 5(4):77-122.
- Erzincioğlu, Y. Z. and D. M. Unwin. 1986. The stability of zoological nomenclature. *Nature* 320:687.
- Evans, T. J. 1914. The anatomy of new species of *Bathydoris*, and the affinities of the genus. Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh* 50(1):191-209.
- Faulkner, D. J. and M. T. Ghiselin. 1983. Chemical defense and evolutionary ecology of dorid nudibranchs and some other opisthobranch gastropods. *Marine Ecology Progress Series* 13(2, 3):295-301.
- Felsenstein, J. 1978. The number of evolutionary trees. *Systematic Zoology* 27(1):27-33.
- Férussac, A.E.J.P.J.F.d'A. de. 1822. *Tableaux Systématiques des Animaux Mollusques classés en Familles Naturelles..etc. Suivis d'un Prodomme Général.* A. Bertrand, Paris. 47 pp.
- Gardiner, A. P. 1936. Engel's paper on "The English Species of the Family Pleurobranchidæ." *Journal of Conchology* 20(7):195-198.
- Ghiselin, M. T. 1966. Reproductive function and the phylogeny of opisthobranch gastropods. *Malacologia* 3(3):327-378. (Year of publication given as 1965 by mistake on paper's title page).
- Gosliner, T. M. 1981. Origins and relations of primitive members of the Opisthobranchia (Mollusca: Gastropoda). *Biological Journal of the Linnean Society* 16:197-225.
- Gosliner, T. M. 1985. Redescription and systematic position of *Pleurobranchaea obesa* (Verrill, 1882) (Opisthobranchia: Pleurobranchidae). *Veliger* 28(1):109-114.
- Gosliner, T. M. and M. T. Ghiselin. 1984. Parallel evolution in opisthobranch gastropods and its implications for phylogenetic methodology. *Systematic Zoology* 33(3):255-274.
- Guangyu, L. and T. Si. 1965. Etude sur les mollusques Pleurobranchidae de la côte de Chine. *Oceanologia et Limnologia Sinica* 7(3):265-277.
- Hartley, T. 1964. Egg laying and early development of *Umbraculum sinicum* Gmelin. *Journal of the Malacological Society of Australia* 1(8):33-35.
- Healy, J. M. and R. C. Willan. 1984. Ultrastructure and phylogenetic significance of notaspidean spermatozoa (Mollusca, Gastropoda, Opisthobranchia). *Zoologica Scripta* 13(2):107-120.
- Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana. 263 pp.
- International Commission of Zoological Nomenclature. 1985. *International Code of Zoological Nomenclature (3rd ed.) Adopted by the XX General Assembly of the International Union of Biological Sciences*. International Trust for Zoological Nomenclature in association with British Museum (Natural History) London and University of California Press, Berkeley and Los Angeles. 338 pp.
- Keen, A. M. 1971. *Sea Shells of Tropical West America: Marine Mollusks from Baja California to Peru*. Edn. 2. Stanford University Press, Stanford, California. 1064 pp.
- Lacaze-Duthiers, H. 1859. Histoire anatomique et physiologique du pleurobranche orangé. *Annales des Sciences Naturelles* 11:199-302.
- McClellan, A. D. 1983. Higher order neurons in the cerebral ganglia of *Pleurobranchaea* have diverse effects on buccal motor patterns. *Journal of Comparative Physiology* 153(4):533-541.
- MacFarland, F. M. 1966. *Studies of Opisthobranchiate Mollusks of the Pacific Coast of North America*. California Academy of Sciences, San Francisco. 546 pp.
- Macnae, W. 1962. Notaspidean opisthobranchiate molluscs from Southern Africa. *Annals of the Natal Museum* 15(15):167-181.
- Marbach, A. and M. Tsurumai. 1973. On the biology of *Berthellina citrina* (Gastropoda: Opisthobranchia) and its defensive acid secretion. *Marine Biology* 21:331-339.
- Marcus, Ernst. 1965. Some Opisthobranchia from Micronesia. *Malacologia* 3(2):263-286.
- Marcus, Ernst and Eveline d. B.-R. Marcus. 1966. The R/V Pillsbury deep-sea biological expedition to the Gulf of Guinea, 1964-65. 9. Opisthobranchs from tropical West Africa. *Studies in Tropical Oceanography* 4(1):152-208.
- Marcus, Ernst and Eveline d. B.-R. Marcus. 1970. Opisthobranch mollusks from the southern tropical Pacific. *Pacific Science* 24(2):155-179.
- Marcus, Eveline d. B.-R. Marcus. 1977. An annotated checklist of the Western Atlantic warm water opisthobranchs. *Journal of Molluscan Studies*, Suppl. No. 4. 22 pp.
- Marcus, Eveline de B.-R. Marcus. 1984. Catalogue of the Western Atlantic warm water Opisthobranchia. 10. The western Atlantic warm water Notaspidea (Gastropoda, Opisthobranchia), Part 3. Umbraculacea. *Boletim de Zoologico, Universidad de São Paulo, Brazil* 9:1-15.
- Marcus, Eveline d. B.-R. 1985. The Western Atlantic warm water Notaspidea (Gastropoda, Opisthobranchia), Part 2. *Boletim de Zoologico, Universidad de São Paulo, Brazil* 8:43-76.
- Marcus, Eveline d. B.-R. and T. M. Gosliner. 1984. Review of the family Pleurobranchaeidae (Mollusca: Opisthobranchia). *Annals of the South African Museum* 93(1):1-52.
- Marcus, Eveline de B.-R. and Ernst Marcus. 1967. American opisthobranch mollusks. *Studies in Tropical Oceanography* 6:1-256.
- Marshall, B. A. 1981. The genus *Williamia* in the western Pacific (Mollusca: Siphonariidae). *New Zealand Journal of Zoology* 8(4):487-492.
- Mazzarelli, G. F. 1898. Contributo alla conoscenza delle Tyloidinidae, nuova famiglia del gruppo dei molluschi tectibranchi. *Zoologische Jahrbücher. Abtheilung für Systematik Geographie und Biologie der Thiere* 10:596-608.
- Minichev, Y. S. 1970. On the origin and system of nudibranchiate molluscs (Gastropoda Opisthobranchia). *Monitore Zoologica Italiano, N.S.* 4:169-182.
- Minichev, Y. S. and Y. I. Starobogatov. 1978. On the systematic arrangement of euthyneuran snails. *Malacological Review* 11(1-2):67-68.
- Minichev, Y. S. and Y. I. Starobogatov. 1979. Peculiarities of the evolution of the reproductive system of the Opisthobranchia and their taxonomy. In: *Sixth meeting on the Investigation of Molluscs. Molluscs. Main Results of Their Study. Abstracts of*

- Communications*. I. M. Likharev, ed. pp. 16-20. Nauka, Leningrad 1979:1-261. (In Russian).
- Minichev, Y. S. and Y. I. Starobogatov. 1984. Taxonomy of Opisthobranchia and peculiarities of the evolution of the reproductive system. *Malacological Review* 17(1-2):112-114.
- Moquin-Tandon, M. G. 1870. Recherches anatomiques sur l'ombrelle de la Méditerranée. *Annales des Sciences Naturelles. Zoologie et Paléontologie* 14:1-135.
- Morse, M. P. 1984. Functional adaptations of the digestive system of the carnivorous mollusc *Pleurobranchaea californica* MacFarland, 1966. *Journal of Morphology* 180:253-269.
- Morton, J. E. 1955. The evolution of the Ellobiidae with a discussion of the origin of the Pulmonata. *Proceedings of the Zoological Society of London* 125:127-168.
- Morton, J. E. 1972. The form and functioning of the pallial organs in the opisthobranch *Akera bullata* with a discussion on the nature of the gill in Notaspidea and other tectibranchs. *Veliger* 14(4):337-349.
- Odhner, N. H. 1926. Die Opisthobranchien. *Further Zoological Results of the Swedish Antarctic Expedition 1901-1903* 2(1):1-100.
- Odhner, N. H. 1939. Opisthobranchiate Mollusca from the western and northern coasts of Norway. *Kongelige Norske videnskaberne Selskabs Skrifter* NR 1:1-93.
- Odhner, N. H. 1968. Sous-classe des Opisthobranches. Systématique. In: *Traité de Zoologie* 5 (3), *Mollusques Gastéropodes et Scaphopodes*. P. P. Grassé, ed. pp. 834-888. Masson et Cie, Paris. (Systematic section of this work collated by A. Franc from Odhner's notes posthumously.)
- O'Donoghue, C. H. 1929. Opisthobranchiate Mollusca collected by the South African marine biological survey. *Union of South Africa, Fisheries and Marine Biological Survey* 7(1):1-84.
- Pelseneer, P. 1894. Recherches sur divers opisthobranches. Parte 1. *Mémoires Couronnés et Mémoires des Savants étrangers, publiés par l'Académie Royale des Sciences, des lettres et des beaux-arts de Belgique* 53:1-157.
- Pilsbry, H. A. 1896. *Manual of Conchology*. Vol. 16. Philadelphia. 262 pp.
- Pruvot-Fol, A. 1954. *Faune de France*. 58. *Mollusques Opisthobranches*. Paul Lechevalier, Paris. 460 pp.
- Pruvot-Fol, A. 1960. Les organes génitaux des opisthobranches. *Archives de Zoologies Expérimentale et Générale* 99 (2):135-223.
- Pruvot-Fol, A. and E. Fischer-Piette. 1934. Sur la *Tylodina citrina* et sur la famille des Tylodiniidae. *Bulletin de la Société Zoologique de France* 59:144-151.
- Rehder, H. A. 1980. The marine mollusks of Easter Island (Isla de Pascua) and Sala y Gómez. *Smithsonian Contributions to Zoology* 289:1-167.
- Rehder, H. A. 1984. The genus *Brondelia* Bourguignat, 1862, and its taxonomic position (Gastropoda: Siphonariidae). *Nautilus* 98(2):83-84.
- Ross, D. R., M. Dale, K. Shields and C. Hulett. 1983. *Taxon Users' Manual*. Edn. P4. CSIRONET Reference Manual 6:1-300.
- Siegler, M. V. S. 1977a. Neuronal basis of *Pleurobranchaea* feeding. *Veliger* 20(1):59-60.
- Siegler, M. V. S. 1977b. Motor neurone co-ordination and sensory modulation in the feeding system of the mollusc *Pleurobranchaea californica*. *Journal of Experimental Biology* 71:27-48.
- Soliman, G. N. 1977. A discussion of the systems of classification of dorid nudibranch veliger shells and their taxonomic significance. *Journal of Molluscan Studies* 43:12-17.
- Sphon, G. G. 1972. *Berthella kaniae*, a new opisthobranch from the Eastern Pacific. *Nautilus* 86(2-4):53-55.
- Thiele, J. 1925. Gastropoda der Deutschen Tiefsee-Expedition, Teil II. *Wissenschaftliche ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer 'Valdivia' 1898-1899* 17(2):38-382.
- Thiele, J. 1931. *Handbuch der Systematischen Weichtierkunde. Erster Band*. Gustave Fischer, Jena. 778 pp.
- Thompson, T. E. 1961. The importance of the larval shell in the classification of the Sacoglossa and the Acoela (Gastropoda Opisthobranchia). *Proceedings of the Malacological Society of London* 34(5):233-238.
- Thompson, T. E. 1970. Eastern Australian Pleurobranchomorpha (Gastropoda, Opisthobranchia). *Journal of Zoology, London* 160(2):173-198.
- Thompson, T. E. 1973. Euthyneuran and other molluscan spermatozoa. *Malacologia* 14:167-206.
- Thompson, T. E. 1976. *Biology of Opisthobranch Molluscs*. Vol. 1. The Ray Society, London. 207 pp.
- Thompson, T. E. and A. Beggington. 1969. Structure and function of the reproductive organs of the three species of *Aplysia* (Gastropoda Opisthobranchia). *Malacologia* 7(2-3):374-380.
- Thompson, T. E. and J. G. Colman. 1984. Histology of acid glands in Pleurobranchomorpha. *Journal of Molluscan Studies* 50(1):65-67.
- Thompson, T. E. and D. J. Slinn. 1959. On the biology of the opisthobranch *Pleurobranchus membranaceus*. *Journal of the Marine Biological Association of the United Kingdom* 38:507-524.
- Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates. *Meddelelser fra Kommissionen for Danmarks Fiskeri - og Havundersogelser, Serie: Plankton* 4:1-523.
- Usuki, I. 1969. The reproduction, development and life history of *Berthellina citrina* (Rüppell et Leuckart) (Gastropoda, Opisthobranchia). *Science Reports of Niigata University. Series D (Biology)* 6:107-127.
- Vayssière, A. 1883. Recherches anatomiques sur les genres *Pelta* (*Runcina*) et *Tylodina*. *Annales des Sciences Naturelles. Zoologie et Paleontologie* 6(15):1-46.
- Vayssière, A. 1885. Recherches zoologiques et anatomiques sur les opisthobranches du Golfe de Marseille - Première Partie, Tectibranchs. *Annales du Musée d'Histoire Naturelle de Marseille - Zoologie. Tome II* 3:1-181.
- Vayssière, A. 1897. Description des coquilles de quelques espèces nouvelles ou peu connues de pleurobranchidés. *Journal of Conchylologie* 44:113-137.
- Vayssière, A. 1898. Monographie de la famille des pleurobranchidés 1. *Annales des Sciences Naturelles. Zoologie* 8(8):209-402.
- Vayssière, A. 1901. Monographie de la famille des pleurobranchidés (Deuxième et dernière partie). *Annales des Sciences Naturelles. Zoologie* 8(12):1-85.
- Wiley, E. O. 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. J. Wiley & Sons, New York. 439 pp.
- Willan, R. C. 1975. Identity and Feeding of New Zealand Notaspidean Opisthobranchs. Unpublished M.Sc. Thesis, University of Auckland. 164 pp.
- Willan, R. C. 1977. A review of *Pleurobranchella* Thiele, 1925 (Opisthobranchia: Pleurobranchaeinae). *Journal of Conchology* 29(3):151-155.
- Willan, R. C. 1978. An evaluation of the notaspidean genera *Pleurobranchopsis* Verrill and *Gymnotoplax* Pilsbry (Opisthobranchia: Pleurobranchinae). *Journal of Conchology* 29(6):337-344.
- Willan, R. C. 1983. New Zealand side-gilled sea slugs (Opisthobranchia: Notaspidea: Pleurobranchidae). *Malacologia* 23(2):221-270.
- Willan, R. C. 1984a. A review of diets in the Notaspidea (Mollusca:

- Opisthobranchia) *Journal of the Malacological Society of Australia* 6(3-4):125-142.
- Willan, R. C. 1984b. The Pleurobranchidae (Opisthobranchia: Notaspidea) of the Marshall Islands, Central-West Pacific Ocean. *Veliger* 27(1):37-53.
- Willan, R. C. and H. Bertsch. 1987. Description of a new pleurobranch (Opisthobranchia: Notaspidea) from Antarctic waters with a review of notaspideans from southern polar seas. *Veliger* 29(3):292-302.
- Willan, R. C. and J. E. Morton. 1984. *Marine Molluscs Part II - Opisthobranchia*. University of Auckland and Leigh Marine Laboratory. 106 pp.